



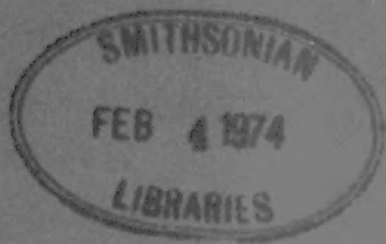
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COMPARATIVE ECOLOGY AND BEHAVIOUR OF
CHAMAELEO PUMILUS PUMILUS (GMELIN)
& *C. NAMAQUENSIS* A. SMITH
(SAURIA: CHAMAELEONIDAE)

By
BRYAN RONALD BURRAGE

Cape Town Kaapstad



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BRYAN RONALD BURRAGE

*South African Museum, Cape Town**

(With 14 figures and 49 tables)

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* Present address: College of the Desert, Palm Desert, California.

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I. INTRODUCTION

This study describes certain aspects of the life history of *Chamaeleo pumilus* (Gmelin) and of *C. namaquensis* A. Smith. Reproductive potential, population size, territorial structure, thermoregulation, behaviour, and other ecological relationships of these chamaeleonids in dynamic equilibrium with their vastly different habitats are considered. The viviparous, arboreal *C. pumilus* lives mostly in mesic areas of southern Africa. The aforementioned ecological considerations of the oviparous *C. namaquensis* have never been studied. This ground-dwelling species inhabits semi-arid and arid areas of southern Africa.

There is no comprehensive picture of chamaeleon ecology. Brain (1961) has given a preliminary picture of the life history and biology of *Chamaeleo dilepis*. Rose (1950) has made general comments on chamaeleons. Ecological studies on field populations of chamaeleons are so few and mostly of such limited scope as to be virtually non-existent. Following his papers on yearly population density variation of *C. pardalis* (Bourgat 1968*a*), and the spermatogenesis cycle of this insular species (Bourgat 1968*b*), Bourgat (1970) has provided a detailed study of *C. pardalis*. These are the only ecological studies on marked field populations of chamaeleons. Bourgat's papers and those of Saint Girons (1962) on sperm storage in female *C. basiliscus*, *C. chamaeleon*, and *C. lateralis*, Wager (1958), Bons & Bons (1960) on reproduction of *C. dilepis* and *C. chamaeleon*, respectively, are the only detailed field studies on chamaeleon reproduction, save short notes by Trench (1912) on *C. calcaratus* (= *C. chamaeleon zeylanicus*) and Menzies (1958) on *C. gracilis*. Chamaeleon colour lability has been the subject of very few serious studies. Until recently the general interpretation of this phenomenon has not altered much from those stated by Aristotle (Crosswell's translation, 1883) and Pliny (Bostock & Riley's translation, 1887). The function of chamaeleon colour lability has been discussed and investigated by Brücke (1852), Weber (1881), Fuchs (1914) and Krüger & Kern (1924). The dynamics of chamaeleon physiological thermoregulation were indicated in studies on the lungs and air sacs by Couvreur & Gautier (1904) and Tornier (1904), and the chamaeleonid carotid body (Adams 1957). Hogben & Mirvish (1928*a, b*) and Zoond & Eyre (1934) investigated colour change in *Chamaeleo pumilus* and *Lophosaura pumila* (both = *C. pumilus*) respectively, and Farghaly (1941) in *Chamaeleo vulgaris* (= *C. chamaeleon*), but few speculated on, or endeavoured to study its functional significance. Some of these early findings of the mediating mechanism of chamaeleon colour lability have been subsequently challenged and enlarged upon by Canella (1963) and Cleworth (unpublished data). There are no field records of chamaeleon body temperatures, but Stebbins (1961) gives body temperature records of captive *C. dilepis* and *C. namaquensis*. Parasites and disease of Madagascan chamaeleons have been studied by Brygoo (1963), Brygoo, Dodin & Sureau (1959) and Chabaud & Brygoo (1960). A fungal infection disturbing the colour lability mechanism is reported by Elkan (1965) for the East African *C. bitaeniatus*.

There are a number of papers based on captive chamaeleons, such as those

by Abel (1931), Angel (1933), Atsatt (1953), Busack & Busack (1967), Bustard (1955, 1958, 1963, 1965, 1966, 1967a), and Von Frisch (1962), which are mostly short and often report results differing from findings on field studies of chamaeleons; a fact which only Bustard (1963) recognized might be true. A detailed discussion of the literature is given in the relevant sections of this paper to which they pertain.

A. *Systematics*

Knowledge of the life history and habits of our commonest reptiles, particularly lizards, is meagre. To avoid confusion as to the life history of which species or subspecies was examined, such studies should follow taxonomic investigations. Nevertheless, in many instances life history studies may help clarify systematics by providing clues to relationships, differences and similarities between closely related taxa. Studies in different areas of a widely distributed species' range help to assess its adaptations to diverse habitats and to determine the validity of recognized subspecies and perhaps the need for establishing others.

The Family Chamaeleonidae (or Chamaeleontidae) forms the Infraorder Rhiptoglossa, which, with the Infraorders Gekkota and Iguania (iguanids and agamids), comprises the Suborder Ascalabota. The Suborder Ascalabota is distinguished from the Suborder Autarchoglossa by the simple body musculature, tongue, and hemipenal structure and generally primitive character of the squamation (Camp 1923). Among the Ascalabota the superior temporal arch of Iguania distinguishes them from Gekkota. The acrodont dentition of chamaeleonids and agamids is sufficient to set them apart from iguanids which have pleurodont teeth.

Many Rhiptoglossa characters are shared with arboreal Gekkota (as partial zygodactyly in *Phyllurus*; reduction of body musculature and hoop-like parasterna in *Uroplates*) and arboreal Iguania (variously independent eye mobility, diverticulate lungs, prehensile tail, anterior pineal foramen, casque development and colour lability in *Agama*, *Anolis*, *Calotes*, *Chamaeleolis*, *Cophotis*, *Polychurus* and *Xiphocercus*). The Cuban iguanid *Chamaeleolis chamaeleontides* is most chamaeleonid-like, with which it shares partly fused eyelids, cranial casque development, and sluggish, deliberate movements (Wilson 1957). Only the Iguania and Rhiptoglossa have developed high laterally compressed arboreal forms. The only really distinctive Rhiptoglossa characters are the highly specialized feet and vermiform, highly extensile tongue, which, in Boulenger's (1885-87) and Gadow's (1901) view, justify their consideration as a separate infraorder; a view rejected by Romer (1956), Terentiev (1961), Mertens (1966) and others, as so many characters on which the separation is based are shared with others of the Infraorder Iguania in which these workers place the chamaeleonids. Cope (1864) was the first to regard the Rhiptoglossa as related to the Agamidae.

Saurians date back to the Upper Triassic; Upper Cretaceous lizards were

essentially modern (Carroll 1969). The fossil record yields no undoubted chamaeleons, and those so assigned are based on jaw fragments with acrodont teeth that could equally be assigned to the agamids, from which the chamaeleonids could be derived (Camp 1923; Romer 1956). Leidy's (1873) *Chamaeleo pristinus* from the Eocene of Wyoming is most similar to the agamid *Calotes*, and thus not a chamaeleon. Camp (1923), Brock (1940), Malan (1946) and others consider chamaeleons as primitive survivors of some ancient pro-agamid-iguanid stock. Hillenius (1963, 1964) feels chamaeleons are of more recent origin, as the most primitive forms (*Chamaeleo chamaeleon* and allies) not only possess the characters one would expect in the hypothetical, ancestral chamaeleon, but also occupy the periphery of the chamaeleonid range (cf. Matthew 1915; Mayr 1954, 1963; Tihen 1949). Shute & Bellairs (1953), Hamilton (1960) and Schmidt (1964) have examined the inner ear structure of lizards to provide clues to their relationships. The latter two consider the chamaeleonid ear primitive—agreeing with Camp, Brock, Malan and others as to chamaeleonid affinities—whereas Miller (1966) thinks the chamaeleonid ear regressed or degenerate and distinct, neither supporting nor rejecting derivation of this group from the agamids, though the chamaeleon cochlear duct could conceivably derive from regression of the agamid type. Thus, most modern evidence indicates the distinctiveness of chamaeleonids, with possible close relationship to the agamids, but rejects the hypothesis that chamaeleons are survivors of an ancient pro-agamid-iguanid stock. This unsolved problem of chamaeleonid origin and affinities is not of further concern. Chamaeleon taxonomy is summarized below.

Terentiev (1961) recognizes 73 species of *Chamaeleo* (= *Chamaeleo*), Mertens (1966) 113 species of *Chamaeleo*, including *Microsaura*. *Chamaeleo* has the tail at least as long as the body, and smooth-scaled soles. *Chamaeleo namaquensis* is a possible exception with its lamellate soles, partly fringed toes, and tail much shorter or equal to body length. Mertens (1966) includes the five species of *Rhampholeon* with the seven species of *Brookesia* (= *Evoluticauda* and *Leandria*, Schmidt & Inger 1965). *Brookesia* and *Rhampholeon* have the tail shorter than the body, and spinose-scaled soles, but *Rhampholeon* differs by having bicuspid claws. *Chamaeleo* embraces the entire range of the Chamaeleonidae and is found in Africa, Madagascar, India, Ceylon, southern Spain, Asia Minor and Arabia; most are arboreal and oviparous. The exceptions are *Chamaeleo chamaeleon* and *C. namaquensis* which are cursorial, even fossorial in desert regions, and the *C. pumilus* and *C. bitaeniatus* groups which are viviparous. *Brookesia*, *sensu stricto*, is confined to Madagascar and is ground-dwelling on fallen leaves in forests. *Rhampholeon* (if a valid genus) is confined to tropical African rain forests in shrubs and undergrowth. The adaptations of chamaeleons show rigid specializations to an arboreal habitat, though some, as *Brookesia*, *sensu stricto*, *Chamaeleo chamaeleon*, and *C. namaquensis* have secondarily reverted to the ground. Chamaeleonids occur from sea-level to the Ethiopian Highlands and Ruwenzori Mountains, inhabiting the littoral to at least the mean high

tide limit (conflicts with Neill 1958), forests, grassland, semi-arid scrub and deserts. Most species average 180 to 350 mm when fully matured (males usually smaller), with extremes of two Madagascan species: *Chamaeleo oustaleti* of nearly a metre, and *Brookesia minima* at 33 mm.

Chamaeleon taxonomy is confusing and best described as in a state of flux. Apart from whether chamaeleonids should be lumped with iguanids and agamids in the Infraorder Iguania or recognized as the separate Infraorder Rhyptoglossa, the family name has been changed several times, principally from Chamaeleonidae to Chamaeleontidae and vice versa, though there has been a myriad of other names and various taxonomic changes.

Gmelin (1789) originally described the Cape dwarf chamaeleon as *Lacerta pumila*, but Daudin (1802) renamed it *Chamaeleo pumilus*, when referring it to the Chamaeleonidae. Gray (1864) recognized Chamaeleonidae as the family name. In the same paper he renamed *Chamaeleo pumilus*, *Lophosaura pumila*. However, *Lophosaura* was preoccupied by a group of South American lizards Gray himself had previously described. Thoughtfully, Gray put the viviparous *melanocephala* (now considered at most a subspecies of *Chamaeleo pumilus*) into the genus *Microsaura*. *Lophosaura* was recognized as valid in subsequent taxonomic revisions, such as those of Methuen & Hewitt (1913), Hewitt (1935) and Power (1932), but since a preoccupied name cannot stand and since *Microsaura melanocephala* was later included in the *pumila* group, the name *Microsaura* took precedence (FitzSimons 1943). Werner (1911), while considering Chamaeleontidae the valid family name, recognized *Chamaeleon* (= *Chamaeleo*) *pumilus*, but not *M. pumila*. Matthey (1931) and Matthey & Brink (1956, 1960) applied cytological technique to what they regarded as chamaeleontids. They found male chamaeleons have no 'Y' chromosome, and showed that *Microsaura* should not be considered apart from *Chamaeleo* and that only one species (*pumilus*) was valid. Skinner (1958) noted the shoulder girdle of *Microsaura pumila* (= *Chamaeleo pumilus*) was more like that of *Chamaeleo* than that of *Brookesia*.

Hillenius (1959, 1963) has reviewed the genus *Chamaeleo* from morphological considerations and co-ordinated these with the cytological findings of Matthey (1931) and Matthey & Brink (1956, 1960). As far as the *pumilus* group is concerned, these workers agree that: (1) *Microsaura* is invalid and referable to *Chamaeleo*. (2) There seems to be one species, *Chamaeleo pumilus*, and the other *Microsaura* species and/or subspecies (e.g. *caffer*, *damaranus*, *gutturialis*, *karrooicus*, *melanocephalus*, *occidentalis*, *taeniobronchus*, *transvaalensis*, and *ventralis*) are best considered no more than subspecies of *Chamaeleo pumilus* until more detailed studies indicate the contrary. Furthermore, *C. p. pumilus* of the southern Cape Province has more characters in common with *C. melanocephalus* than with its subspecies *C. pumilus transvaalensis*. *C. p. transvaalensis* shares more characters with *C. v. ventralis*, *C. ventralis occidentalis* and *C. damaranus* than with *C. p. pumilus*. The hemipenes of *C. pumilus* are of the 'cogwheel' type as in *C. dilepis* (Broadley 1971). The viviparous South African *C. pumilus* group is

distinct from the viviparous East African *C. bitaeniatus* group. Therefore, there is no validity in the arguments of Methuen & Hewitt (1913) and Power (1932) for re-establishment of a separate genus (*Lophosaura* and *Microsaura* as per Gray, 1864).

Hillenius (1959, 1963, 1964) investigated distribution of characters, not of species, and showed that East Africa has the greatest number of characters, and, hence, is the origin of *Chamaeleo*, with secondary centres in Madagascar and West Africa. Away from East Africa the number of shared characters diminishes. Thus, while Madagascar has the bulk of chamaeleonid species and the greatest variety of form and size, it is not the original home of *Chamaeleo*, and chamaeleonids flourish there because of the absence of higher predators as well as competitors. Hillenius (1959, 1963) showed that earlier taxonomists wrongly assigned characters as 'key' because they had not studied the whole group and often recognized species on few specimens, or even one, and in some cases confused sexual dimorphism with their 'key' characters, which they often did not apply uniformly, assigning females to one genus or species and the males to another. Mertens (1966) endorses Matthey's (1931), Matthey & Brink's (1956, 1960) and Hillenius's (1959, 1963, 1964) views in determining subdivisions of the form-rich and unwieldy *Chamaeleo*, and hopes the procedure will be extended to *Brookesia* to better understand taxonomic relationships within the chamaeleonids (or chamaeleontids). Mertens agrees recognition of *Microsaura* is unwarranted until a study of all forms is made, and currently validity of *Microsaura* cannot be recognized on purely nomenclatural views alone. Mertens feels a study of the *pumilus* and *dilepis* complexes will raise rather than diminish the 113 species of *Chamaeleo*. For this investigation, the nomenclature of Daudin as validated by Hillenius and Matthey is endorsed.

A. Smith (1831) originally described the Namaqualand chamaeleon as *Chamaeleo namaquensis*. Fortunately, *C. namaquensis* is harder to find than other chamaeleons, thus largely escaping the taxonomic confusion perpetrated on *C. pumilus*. After several questionable changes, Gray (1864) finally placed *namaquensis* in its own genus, *Phumanola*. Werner (1911) placed *namaquensis* in *Chamaeleon*. FitzSimons (1943), Hillenius (1959, 1963) and Mertens (1955, 1966) call it *Chamaeleo namaquensis*. Hillenius (1959) feels that *Chamaeleo namaquensis*, while previously considered as very isolated and not closely related to other species, is in fact more or less related to the *Chamaeleo chamaeleon* group in homogenous squamation, sometimes with scales in rosette-shaped groups, no temporal crest, casque as *Chamaeleo basiliscus* (roof-shaped parietal crest higher than lateral crests, elevated posteriorly, lateral crests stopping just after the temporal region, no occipital lobes). *Chamaeleo namaquensis*' dorsal knobs are very similar to those of the Camerounian *Chamaeleo wiedersheimi*, whose position is unknown because of insufficient material, but is similar to *Chamaeleo namaquensis* in several characters. Since *Chamaeleo dilepis* is in the *Chamaeleo chamaeleon* group, its link with *Chamaeleo namaquensis* makes sense from the point of distribution.

B. *Distribution and habitat*

Chamaeleo pumilus is of southern African distribution, occurring from Lüderitzbucht, South West Africa (ignoring an introduced population at Walvis Bay), south through the Cape Province and north through Natal to the north-east Transvaal (FitzSimons 1943, 1965; Hillenius 1959; Mertens 1955, 1966). For an arboreal chamaeleon it is of ubiquitous habits and habitat, inhabiting the extremes of desert shrubs of Namaqualand and the Karoo and the high rainfall areas of the south-east coast and Drakensberg plateau.

Chamaeleo namaquensis ranges from southern Angola through South West Africa from the Atlantic shore to the east of the Great Western Escarpment and south through karoid parts of the Cape Province (FitzSimons 1943; Hillenius 1959; Mertens 1955, 1966). It inhabits arid and semi-arid situations, some of which seem an unlikely 'chamaeleon' habitat. One of the few ground-dwelling chamaeleons—*Brookesia* of Madagascan tropical rain forests is another—it is one of two chamaeleons to invade strict desert. The other deserticulous chamaeleon is the ubiquitous Mediterranean variety (*Chamaeleo chamaeleon*), to whose group *C. namaquensis* is probably related. Alexander's (1838) description of *C. namaquensis* at Walvis Bay still holds true for an introduction: 'When [approached] these cameleons [*sic*] . . . opened their mouths . . . and bissed like angry snakes, whilst a bag under their mouth swelled to a great size, which, with their dark blotched bodies, gave them a hideous appearance. They run fast, and are accounted to be poisonous by the natives.' Alexander's description is correct, for they can run at a quick walk and their high speed evasions make flight a satisfactory escape for this chamaeleon.

This study was largely motivated by the virtual dearth of knowledge on chamaeleon ecology. In essence, this paper presents two autecological studies on the mesic-adapted *Chamaeleo pumilus* and the xeric-adapted *C. namaquensis*. The problem of the role of body compression and colour change was investigated in the field and in the laboratory, as was the dynamics of chamaeleon physiological thermoregulation in maintaining these animals in thermal equilibrium with their respective environments. A study of chamaeleon habitats was undertaken to see if they were of ubiquitous or restricted habitat preferences. The reproduction of the oviparous *C. namaquensis* and viviparous *C. pumilus* was thoroughly investigated under natural conditions and supplemented with laboratory records. A complete idea of chamaeleon reproduction was acquired from courting to maturity of the young. The reproductive potential was integrated with field studies on mortality, population dynamics, spatial organization, and behaviour. A detailed investigation was made on nutrition needs and prey items, and water and salt metabolism. The last study was particularly interesting, since *C. namaquensis* inhabits the desert littoral, ingesting food of high salt content, the salt being excreted via a nasal salt gland. The study of adaptation to desiccation in both chamaeleons provided valuable information on their respective solutions to water balance and water sources.

After preliminary field studies on chamaeleon requirements, conditions

for successfully maintaining captives were improved, allowing laboratory findings to complement field studies. Since captive chamaeleons usually do poorly, this casts considerable doubt on the acceptance of previous findings on captives. Thus, in this study an attempt was made to integrate laboratory and field investigations to give as complete an understanding of the ecology and environmental adaptations of at least two chamaeleonids.

II. MATERIALS AND METHODS

A. Collecting and observational methods

Specimens of *Chamaeleo pumilus* were collected and observed from 13 January 1969 to 30 November 1970, chiefly at Stellenbosch, but also at Beaufort West, The Strand, Van der Stel, and in the Cape Peninsula in the Cape Province. They were readily found on garden shrubs, bushes, grasses, and on reeds along the margins of various bodies of water in developed and undeveloped areas.

Specimens of *C. namaquensis* were observed and collected during 1969 in April, June, August and November, and in February 1970 in South West Africa. Inland populations of *C. namaquensis* were investigated at Gobabeb, Tsondab, Geluk Farm, Solitaire and Rehoboth, and coastal populations from Walvis Bay north to Cape Cross.

C. pumilus and *C. namaquensis* would not enter any sort of trap, requiring employment of random and sector search methods. In the latter method, a given area was intensively searched in the morning, collecting, taking data from the animals present, while noting signs and marking the site. The afternoon search sector was reached by walking to it via the morning sector, checking on the markers to see any fresh signs or, hopefully, the animals themselves. This method proved quite rewarding. These patrols were more or less straight lines and selected through varied habitats. Return was by a parallel route. The maximum daily return distance covered was 25.75 km, the minimum 12.88, the average 19.31. Shorter trips with observation points were also employed, especially for social interaction, activity, and territorial studies. The sites to which animals were retreating for the night were marked on the return afternoon sector search, for later observations during the night. Binoculars were employed for observing both species from a distance.

Animals were marked by branding an identity number on the proximal ventrum of the tail, or by small identity number-bearing leg bands. Chamaeleons were first cooled to render them comatose, and restrict peripheral circulation to minimize bleeding when the number was applied with a sterilized surgical blade. Both methods were durable and effective. A total of 165 (87 ♂♂, 78 ♀♀) coastal and 42 (22 ♂♂, 20 ♀♀) inland *Chamaeleo namaquensis* adults were marked, and 107 coastal juveniles. A total of 494 (159 ♂♂, 187 ♀♀, 148 juveniles) *C. pumilus* were marked at Stellenbosch. These animals were never killed or collected, serving as subjects for field territorial, behavioural, and reproduction

studies. Reproduction data were obtained by palpating. Prey preferential studies were also gathered from them by observation and scat analysis.

B. Thermal studies

A Wesco rapid equilibrium cloacal thermometer was used to obtain most lizard field temperatures, though a Yellow Springs Instrument 46TUC Telethermometer (probes YSI 402 body; 405 air temperature; 409 skin surface; 524 subdermal) was employed, occasionally in the field, and exclusively in all laboratory studies on thermoregulation, metabolic, and cardiac rates. Since colour change of chamaeleons is rapid and alters the skin temperature, all skin temperatures must be recorded as rapidly as possible. The telethermometer is the superior instrument, since it records temperatures almost instantly, and several probes can make simultaneous recordings. However, by simultaneously calibrating telethermometer readings with those made by a thermometer, a technique was devised to reflect most accurately all chamaeleon temperatures. All skin temperature readings (first, side to the sun; second, side in the shade) must be made as soon as possible, and precede cloacal readings. The skin surface temperatures must be made in such a manner that the chamaeleon is not greatly alarmed. For example, a pale chamaeleon on a hot day is reflecting heat, and the temperature of the skin presented to the sun is at or near that of the air temperature. If angered, such a chamaeleon goes uniformly black in less than 1,6 seconds, and almost instantly absorbs heat ($\geq 3,0$ C rise in skin surface temperature within 30 seconds). *Chamaeleo namaquensis* and *C. pumilus* did not evince more than alertness if approached slowly and skin surface temperatures recorded gently. Though the cloacal temperature lags in reflecting the skin surface temperature, all cloacal readings must be made within 10 seconds of capture, and all readings employing a cloacal thermometer must be completed within 20 seconds, cloth insulating the chamaeleon during the reading to eliminate temperature exchange between the investigator and subject. All chamaeleon and environmental temperatures were recorded in the shade of the author's body. Data were not used from injured chamaeleons, those forced to remain in the shade or open by the author's activity, or those that were not readily captured or overtly disturbed.

Various substrate and air temperatures were recorded in the field to assess their bearing, if any, on chamaeleon body temperatures. Surface substrate temperatures were taken by resting the recording instrument on the surface. Temperatures at subsoil depths of 0,5; 2,0; 5,0; 10,0; 15,0; 20,0; 25,0 and 30,0 cm were taken by pushing the recorder down until the desired depth was reached. Air temperature was taken at two metres (T_{a2m}) and fifty millimetres ($T_{a50\text{ mm}}$) from the substrate surface, or what the animals were on. Environmental temperatures (T_e) were the same as the $T_{a50\text{ mm}}$ reading in the case of *Chamaeleo pumilus*. Environmental temperatures in the case of *C. namaquensis* varied according to what the animals were on (rock, gravel or sand surfaces), the vegetation-protected temperature of the substrate surface (T_s), the vege-

tation-protected T_{a50} mm when in or on a plant, and the T_s of the lee, crest, or windward of hummocks. Details of weather, cloud cover, wind velocity and direction, and sunrise and sunset were also recorded. All such weather data collected from 13 January 1969 to 30 November 1970 were divided into 'cool' (April to September) and 'warm' (October to March) months, and further subdivided into 'fair' (0–29% cloud or fog), 'overcast' (29–100% cloud or fog), and 'rainy' weather lasting throughout the day. For coastal Namib readings, the condition of early morning and late afternoon fog with clear midday skies, necessitated the category of 'partly overcast'.

A laboratory experiment of thermoregulation was designed to test the role of body compression and skin colour in light and total darkness. A light-proof temperature room (effective ambient temperature: -5.0 to 40.0 C) was used, so that the animals could be tested over the same temperature range in total darkness and in light, and in light followed by dark and so on sequentially. Radiant heat and light from a uni-directional source, as with the sun, was employed, except in dark conditions when just heat was used. Ten animals of each species, two at a time (one of each species), were secured by tape to a board (160×70 mm) in such a manner that they could compress and position the body freely and stand up, stiff-legged, but not walk off. The board and the animals were supported by a ring stand 300 mm from the counter surface. Thirty-minute intervals at each temperature (-4.5 ; 2.5 ; 5.7 ; 15.0 ; 17.0 ; 18.0 ; 25.0 ; 30.0 ; 35.0 ; 42.0 C with light) (-5.0 ; 5.3 ; 8.6 ; 12.0 ; 13.8 ; 14.6 ; 20.3 ; 23.0 ; 30.1 ; 40.0 C in the dark) were used to conform with previous colour studies, though results at ten-, twenty-, and sixty-minute intervals were virtually identical. Trial runs were conducted for a week to allow the subjects to become accustomed to the protocol. In the dark, instrument readings were made with a flashlight, screened from the subjects. Ambient air temperature, skin surface and chamaeleon body temperatures were recorded at each time interval, along with notes as to body compression, skin colour, and behavioural state of the subjects.

A second temperature test was set up in an outside enclosure (3×2 m) to examine body compression and skin colour in thermoregulation under 'natural' conditions. The floor was red Namib dune sand 150 mm thick in which was embedded a pot containing a small acacia plant. Ten specimens each of *Chamaeleo namaquensis* and *C. pumilus* were used. The plant was provided for *C. pumilus*, which will not climb down from, and is at ease when a raised object is available. Adult *C. namaquensis* will not climb. Substrate temperatures were recorded as well as the readings made in the previously described experiment. Telethermometer leads were made sufficiently long enough to allow the animals complete freedom of movement and action. Data from two animals of each type could be recorded simultaneously. Five days were allowed for the subjects to become accustomed to the set-up, followed by ten days of data-taking. Suitable precautions were taken to allow as many animals as possible to be used without causing territorial stress that would affect colour and compression changes.

Preferred temperature tests were run on both species (18 *Chamaeleo namaquensis*, 20 *C. pumilus*) at ambient temperatures of 5,0 to 50,0 C in long, runway-type cages 3 × 2 m which were placed horizontally for *C. namaquensis* and vertically for *C. pumilus*, in order to house a small potted plant for the convenience of the latter. Red Namib dune sand arranged in banks of various depths (50–300 mm), and scattered rocks provided shelters. Thus, by such arrangements, spatial behaviour of both forms was also realized. Instrumentation and readings recorded were as in the previously described experiments. Preferred temperature tests were run for two weeks, after allowing the subjects a week to get used to the arrangement and select space preferenda.

The role of the skin in mediating core temperature changes in chamaeleons was examined at various ambient temperatures from 5 to 35 C at 10 degree intervals. Water blebs were injected subdermally in ten *Chamaeleo pumilus* and eight *C. namaquensis* and subdermal thermistor probes inserted on both sides of the body of each chamaeleon and another probe inserted into the large intestine of each subject. Skin surface, subdermal, body, substrate, and air temperatures were then read from the telethermometer at a given temperature interval, and the colour of both sides of the body, body compression, and other notations recorded. The same test was run on five dead and five live individuals of each species to assess heating and cooling rates at a given temperature in live and dead chamaeleons.

C. *Metabolic rate studies*

A device as described by Bailey, Kitts & Wood (1957) was employed and their procedure followed, except that the equilibration time was lengthened to thirty minutes. The value of this device is the ease with which oxygen consumption can be measured at various activity levels over any time interval.

Chamaeleons struggle violently if restrained in a submerged vessel, so telethermometer leads were made sufficiently long enough to ensure maximum freedom of movement. Readings at rest were possible, and since the subjects periodically sought active escape, various activity states could be measured, such as torpor, sleep, awake but alert, and active. The animal vessel was provided with a small twig for the convenience of *C. pumilus*.

Oxygen consumption from 5,0 to 45,0 C was measured, and apart from 40 to 45 C, ten degree temperature intervals were employed. Recording instrumentation for temperatures was as in the previously described thermoregulation experiments. Air temperatures of both the animal and blank vessels were recorded, as well as the body temperatures of the animals. Also recorded were the respiration rates, body compression, and skin colour of the animals, and when they commenced panting. At temperatures other than 20 C, a nearby oven and refrigerator were used to hold, raise, or lower subjects' temperatures to the test level. A period of 205 minutes was necessary to bring *C. namaquensis* body temperatures down from 20 C to 5,0 C and 100 minutes for *C. pumilus*. Sixty minutes were needed to raise *C. namaquensis* body temperatures from 20 to

40 C and 35 minutes for *C. pumilus*. Difficulties were encountered bringing *C. pumilus*, except for two, to 45 C. Fifteen *C. pumilus* ranging from 5.1 to 24.7 g ($\bar{x} = 11.4$); and 15 *C. namaquensis* ranging from 49.3 to 113.4 g ($\bar{x} = 76.1$) were used. Rehearsal runs were conducted for a week to allow subjects and experimenter familiarization with technique and equipment. Recordings were made from 08:00 to 18:00 hours, with test temperatures temporally varied to eliminate any circadian rhythm effects. Results were corrected to standard temperature and barometric pressure.

D. Cardiac rate studies

The relationship of chamaeleon heart rate to temperature was also investigated. Five *C. namaquensis* (71.6–115.0 g; $\bar{x} = 80.0$) and five *C. pumilus* (6.0–26.0 g; $\bar{x} = 13.0$) were used. Ten degree temperature intervals from 5.0 to 45.0 C were employed, animal body temperatures being held, raised, or lowered as previously described. During experimental runs, a pan containing ice was placed under the subjects to keep ambient temperatures low, and a red lamp 0.5–1.0 m away was employed for higher temperatures. A small twig was necessary for the *C. pumilus* to cling to. The animals were placed in a container 660 × 300 × 300 mm open to the experimenter on one side. Body and air temperatures were monitored as in the previously described experiments, and a Stanley Cox Electrocardioscope (Med 158) recorded heart beat. Familiarization runs were conducted for a week for the specimens to become used to the procedure.

E. Food studies

In calculating the amount devoured by 25 captive *Chamaeleo namaquensis*, 35 captive *C. pumilus*, and chamaeleons in the field, food was measured by volumetric water displacement and arranged by size from very small (< 0.25 ml; 2–3 mm long), small (0.25 ml; 10 mm long), medium (0.75 ml; 20 mm long), large (2.0 ml; 30 mm long), to extra large (4.5 ml; 54 mm long), respectively Food Indices 1–5. Marked prey was given to chamaeleons at different times to determine rates of passage.

Prey taken by wild chamaeleons was studied by sacrificing the following: *C. pumilus* (February, 6 ♀♀, 3 ♂♂; March, 6 ♀♀, 6 ♂♂; April, 9 ♀♀, 8 ♂♂; May, 8 ♀♀, 8 ♂♂; June, 10 ♀♀, 6 ♂♂; July, 10 ♀♀, 5 ♂♂; August, 7 ♀♀, 8 ♂♂; September, 7 ♀♀, 5 ♂♂; October, 7 ♀♀, 3 ♂♂; November, 5 ♀♀, 5 ♂♂; December, 6 ♀♀, 4 ♂♂; January, 5 ♀♀, 4 ♂♂; 1969–1970), and *C. namaquensis* (April, 9 ♀♀, 5 ♂♂; June, 14 ♀♀, 9 ♂♂; August, 5 ♀♀, 4 ♂♂; November, 11 ♀♀, 6 ♂♂; February, 11 ♀♀, 6 ♂♂; 1969–70). Animals were collected in the morning and afternoon when they were adjudged to have eaten, but not yet digested their meal. Chamaeleons were killed by decapitation and then preserved in 70% alcohol, with exact date, time, and locality. Length of the stomach, small and large intestine were measured in millimetres with Vernier callipers or measuring dividers. Stomach contents were removed, weighed on a Mettler H10T balance

and placed in vials with identifying labels for future analyses. Scats provided a valuable source of prey information for both species, particularly *C. namaquensis*. *C. namaquensis* scats are large (up to 60 mm long) and very distinct. They last in the wind and shifting sands for about three days, though only those no more than two days old were taken. Fresher ones formed the bulk of scats examined. Scats were collected and processed in the manner previously described for stomach contents. The percentage of items in stomach contents and scats was calculated by volumetric analysis. Endoparasites were also removed from the digestive tract, placed in 70% alcohol and sent to Dr Prudhoe of the British Museum (Natural History) for identification.

F. Water and salt balance studies

Ten *Chamaeleo namaquensis* (17,8–90,1; \bar{x} = 58,1 g) and ten *C. pumilus* (6,4–12,4; \bar{x} = 9,2 g) were fasted but hydrated for 24 hours prior to use in a desiccation study. They were then weighed on an Ohaus animal scale and placed one each in glass desiccation chambers (0,20 m diameter) in zero per cent humidity created by silica blue gel crystals below and separated from the animals. The lips of the chambers were sealed with silicon grease. A small twig, pre-dried in an oven, was provided for the *C. pumilus* to cling to. The test was run for seven days at $25,0\text{ C} \pm 1,3$ in a temperature room, the chamaeleons subjected to eight hours of light per day. Faeces and uric acid were removed daily and weighed (Mettler H10T balance). Wastes were removed early in the morning at such time when fasting chamaeleons always had eliminated. Each chamber was aerated daily. At the end of seven days, all animals were weighed and a half of each species group were killed. Blood samples were taken from this dehydrated group in haematocrit capillary tubes and centrifuged on a clinical centrifuge at 2 500 rpm for thirty minutes. A second blood sample, taken in polyethylene microtest tubes, was centrifuged at 10 000 rpm for five minutes to obtain plasma for freezing point determination of osmolality. The remainder of each species were given as much water as desired and the following day weighed and killed, the previously described procedure for the dehydrated group being followed.

A separate study lasting twelve days examined survival with food but no water. The animals were placed in a separate cage maintained at $25,0\text{ C} \pm 3,2$; and 40–50% humidity. Eight *C. pumilus* (6,1–14,9; \bar{x} = 9,7 g) and seven *C. namaquensis* (36,0–91,4; \bar{x} = 61,7 g) were weighed at the start, every third day and at the conclusion of the study. Faeces and uric acid were collected as soon as they were eliminated and weighed as previously described, and blood and plasma taken as previously from two *C. pumilus* and two *C. namaquensis* on the twelfth day. The survivors were dehydrated and body weights taken daily as were the weights of any droppings. At day 15 the survivors were killed, being processed as previously described.

Blood was similarly taken from seven freshly caught *C. pumilus*, and seven inland and ten coastal *C. namaquensis* for haematocrit and osmolality plasma

determinations. For *C. pumilus* analysis was immediate, but for *C. namaquensis*, except for haematocrits, analysis was one to three days after capture.

The osmolality of chamaeleon plasma was determined by measuring the comparative melting point against standard solutions (100; 325; 500 and 900 mOsm) in the manner of Gross (1954).

The exudate from the nares of *Chamaeleo namaquensis* suggested the presence of a nasal salt gland, the nature of which was grossly examined but not so histologically. An exudate sample was examined by Dr V. Wolfe, Department of Chemical Pathology, University of Stellenbosch, using a flame photometer.

G. Territorial and population studies

The method employed for the iguanid *Uta stansburiana hesperis* (Burrage 1966) was adapted for chamaeleon territorial studies and was especially valuable for *Chamaeleo namaquensis*. This method allows territorial investigations and population structure to be studied together. Close daily observation throughout the day gave an accurate picture of the spatial arrangement of chamaeleons, not only in regard to the extent of the territory of individuals, but also those parts most used. The open desert facilitated distant observations by binoculars from a vantage site. Points visited by a chamaeleon were marked at the site, the lizard's number, sex, and date being printed on a marker in waterproof ink. The points were simultaneously plotted on a scaled map on graph paper of the given area. The denser the dots, the greater the activity of the lizard within a given part of its occupied area, and the peripheral dots on the map and site markers gave the exact area. Connecting the outlying dots gave the periphery of the territory, the area of which was then computed with a planimeter from the graph paper. Territorial conflicts and social interactions were marked on the site on which they occurred and on the graph paper to determine usage of a given territory and which part(s) were most vigorously defended.

H. Reproduction studies

Those *Chamaeleo pumilus* and *C. namaquensis* used in food studies also served for anatomical examinations of reproductive state. Each chamaeleon was tagged with the date, precise locality of collection, and observational data. Chamaeleons were weighed on a Ohaus animal scale and then killed, whereupon various measurements were taken with measuring dividers. All *C. pumilus* and most *C. namaquensis* were freshly dissected and their reproductive structures studied. Those *C. namaquensis* not studied immediately after death, were stored in 70% alcohol. The maximum delay in examination was seven days. The chamaeleons, their reproductive structures, embryos (*pumilus*), eggs (*namaquensis*) were measured with Vernier callipers or measuring dividers in millimetres. The reproductive structures were weighed on a Mettler H10T balance. These excised parts were fixed in 10% and preserved in 4% formalin. Routine histological techniques were carried out on some of these reproductive tissues

which had been embedded in paraffin wax. Sections were cut to 5 or 8 μ and stained with haematoxylin-eosin, or azo-carmin and azan.

In order to examine the role of the fat bodies in reproduction, a group of six *Chamaeleo pumilus* and four *C. namaquensis* females and four males of each species had their fat bodies excised. Four controls in each species category group were sham-operated. The animals were cryo-anaesthetized and kept comatose during the operation by being placed ventrum up on a plastic bag filled with crushed ice in which was moulded a hollow to accept each subject. Sterile instruments and technique were employed. Cautey sealed the severed areas, and sterilized adhesive 'butterflies' closed the wounds.

In order to examine the role of the corpora lutea, five pregnant female *Chamaeleo pumilus* had their corpora lutea excised, with another five sham-operated as controls. Four gravid *C. namaquensis* had their corpora lutea excised, with an additional four sham-operated as controls. The operative technique was as previously described for fat body excision.

III. RESULTS AND DISCUSSION

A. *Habitat of Chamaeleo pumilus*

Chamaeleo pumilus inhabits any vegetation guaranteeing a plentiful and sustained prey source, such as flowering bushes and hedges, grasses, supratidal bushes and grasses, and especially reeds surrounding stagnant bodies of water. *C. pumilus* was observed in the Cape Province, in the southern Namib Desert at Port Nolloth, the semi-arid Karoo at Leeu-Gamka and Beaufort West, and the south-west Cape winter rainfall area at Stellenbosch, Van der Stel station, and The Strand. The vegetation at Port Nolloth is West Coast Strandveld, consisting of open, semi-succulent scrub of Fynbos form and intermediate between the Coastal Fynbos and the Succulent Karoo. The Karoo vegetation is complex, consisting of succulents, and semi-arid shrubs. The winter-rainfall area has evergreen shrubs, with a variety of grasses and other annuals. A full discussion of the vegetation of all these areas is given by Acocks (1953).

B. *Description of study stations of Chamaeleo pumilus*

Stellenbosch is situated in gently rolling lowland at the mouth of the Jonkershoek Valley. Data were taken from *Chamaeleo pumilus* inhabiting the University of Stellenbosch Botanical Gardens, suburban hedgerows and gardens, which are planted with many exotics, and from the Marais Park with natural shrubs. *C. pumilus* was also studied in vegetation surrounding freshwater bodies, roadside and railroad right-of-way ditches (Fig. 1), where reeds, mostly *Phragmites*, predominate. Van der Stel station and The Strand occupy inland and coastal situations respectively, on the gradually seawards sloping base of the Hottentots Holland range. *C. pumilus* is abundant in the reeds along the railroad right-of-way at Van der Stel station, and supratidally on the backshore shrubs and grasses at The Strand.

Weather data for the principal study station of Stellenbosch are presented in Table 1, from data provided by the Geography Department of the University of Stellenbosch. During 1969-70 rainfall was approximately two-thirds normal, though the preceding years had average precipitation. Stellenbosch has a winter-rainfall climate with the bulk of the rain falling in winter, though not entirely limited to it. North-west winds bring rain; south-westerly clearing with showers to fine; south-easters are strong winds.

Table 1. Weather data for Stellenbosch, Cape Province, Republic of South Africa (source, Geography Department, University of Stellenbosch).
Temperatures are in degrees Celsius; rainfall in millimetres.

	Temperatures				Monthly Mean	Rainfall
	Absolute Max.	Min.	Mean Max.	Min.		
1969						
January . . .	33,7	8,5	26,0	13,2	19,6	41,9
February . . .	36,0	9,4	28,1	14,3	21,2	23,5
March . . .	41,1	9,5	27,6	14,4	21,0	38,5
April . . .	26,6	4,1	20,9	10,3	15,6	45,9
May . . .	26,0	3,5	20,1	6,6	13,3	17,1
June . . .	26,6	1,7	16,6	6,4	11,5	91,3
July . . .	25,6	1,0	16,5	5,1	10,8	71,9
August . . .	29,4	2,0	18,2	7,0	12,6	85,6
September . . .	28,9	1,0	18,0	5,6	11,8	88,4
October . . .	34,4	6,5	20,5	9,9	15,2	66,1
November . . .	33,3	6,0	24,0	10,2	17,1	16,7
December . . .	36,7	7,0	27,3	12,8	20,0	8,0
1970						
January . . .	37,8	10,1	28,5	13,9	21,3	8,9

The native vegetation is macchia shrub of Coastal Rhenosterbosveld (Acocks 1953), of which rhenosterbos (*Elytropappus*) is distinctive. There is a variety of undershrubs, grasses, and other annuals. On beaches and disturbed areas succulents such as *Mesembryanthemum* predominate. Over the years much native vegetation has been destroyed and the area planted with exotic trees.

Reptiles preying on *Chamaeleo pumilus* are discussed in the predation section (see p. 32), and this discussion deals with co-inhabiting reptile competitors of *C. pumilus*. The most important reptilian competitor of *C. pumilus* is the skink *Mabuya capensis*, which is of ubiquitous habits and, while primarily ground-dwelling, frequently ascends into and hunts prey in shrubs inhabited by chamaeleons. It appears less in evidence in grassy and reedy areas, where it does not climb into such vegetation. A large skink might prey on any newborn *C. pumilus* encountered. *C. pumilus* was rare in exotic montane conifers, but was common in such trees in lowland areas. Montane conifers are abundantly inhabited by geckos (*Phyllodactylus*), which might prevent *C. pumilus* from successfully invading this niche. However, montane areas might represent marginal habitat to *C. pumilus*, since the largest concentrations of chamaeleons in uplands were limited numbers on shrubs on sunny slopes and streamside vegetation.



Fig. 1.

Chamaeleo pumilus habitat on reeds, mostly *Phragmites*, growing in ditch beside railroad right-of-way (Stellenbosch goods yards).

C. *Habitat of Chamaeleo namaquensis*

Mr John Visser found a large *Chamaeleo namaquensis* on the road near Laingsburg, Cape Province, and it is recorded from the arid and semi-arid (Fig. 2A) portions of the Cape Province. The author studied them in the most arid part (that between 18° to 29° South latitude) of the central Namib Desert (Meigs 1966) of South West Africa along the coast from Walvis Bay north to Cape Cross, in the interior at Gobabeb and Tsondab, the edge of the Great Western Escarpment at Geluk Farm and Solitaire, and the South African Plateau highlands at Windhoek and Rehoboth. The geography and other vitae of this area are given by Meigs (1966), Koch (1961), Logan (1960), Schulze (1969) and the *South West Africa handbook* (1971-2); the first three containing pertinent literature to more detailed studies. The plateau and Great Western Escarpment are better-watered, supporting grasses and scattered thorn trees (Fig. 2B) on the uplands and steppe along the escarpment. Vegetation rapidly becomes sparser farther west to the Atlantic, and in the true Namib is meagre and may be absent. Around mountains, and along watercourses the 'luxuriance' of vegetation varies according to the water supply from riverine forest along the Kuiseb River to a better showing of succulents along washes.

D. *Description of study stations of Chamaeleo namaquensis*

The principal study areas were the coastal central Namib Desert from Walvis Bay to Cape Cross, based at Swakopmund, and the interior, based at

the research station at Gobabeb, 120 km south-east of Walvis Bay and about 58 km from the Atlantic. Sorties were made to surrounding areas from these bases. General descriptions of these regions are given by Logan (1960), Koch (1961) and Meigs (1966). Dunes, mountains and gravel plains are the principal biotopes, with special biotopes of hygrophilous or halophilous strata, for example, river beds and pans.

That part of the littoral Namib (Fig. 5A) studied is primarily sandy beach with occasional outcrops of the underlying Namib bedrock platform, and massive deposits of fly-infested tidal wrack. The backshore is a monotonous expanse of soft, dirty gray-white gravel, virtually devoid of plants. South of the Swakop River are dunes lying east of the coastal rail line, over which they occasionally drift. Proximal to the beach are small (about 10 m high), whitish gray seif dunes devoid of vegetation. Further inland, especially near Walvis Bay, the coastal dunes (Fig. 6A) are considerably larger (about 200 m high), yellow, and support sparse vegetation.

The north bank of the Swakop River consists of barren, flat-topped limestone bluffs (Fig. 6B). The base of this outcrop has a skirting deposit of wind-blown dune sand. Away from the outcrop is the monotony of the featureless gravel plains (Fig. 5B) unbroken except for slightly indented meandering washes. Farther north the monotony of the gravel plain is broken by broad-based, narrow-ridged outcrops of black diorite and white dolomite. South of the Swakop River gravel plains form corridors between dune ridges.

The Swakop River bed (Stengel 1964) consists of river channel, flats (Fig. 4B) and varied sized hummocks (Fig. 7A) of whitish sand. These river hummocks may be single or inter-connected as a miniature mountain range. Stengel's Map 1 graphically shows the area of dune hummocks (Fig. 7B) in the Swakop River bottomlands, which mostly lie south of a 1.3 m high bank and the coastal dunes. These hummocks are composed of wind-blown dune sand and are of varied size, but not as large as the river hummocks, nor interconnected. Dune hummocks reach a maximum height of 2.3 m and river hummocks 3.5 m.

At the principal central Namib Desert interior site of Gobabeb are located featureless gravel plains, with occasional granitic outcrops (Fig. 3A), large reddish dunes (Fig. 3B), with basal vegetation (mostly *Aristida* grasses), the riverine forest of the Kuiseb (Fig. 4A), granitic mountains (Fig. 3A), such as Zwartbank and Rooikop, and sandy flats, with scattered grass clumps. Further descriptions of the physiography are given by Logan (1960), Koch (1961) and Meigs (1966).

Table 2 gives air and substrate temperature data for the coastal and interior central Namib and is derived from data collected by the author, those collected at Swakopmund by Mr Moisel for the Namib Desert Research Station, and by the Namib Desert Research Station at Gobabeb for the interior. These data are in addition to those made for environmental and body temperatures collected for the chamaeleons, and thus there are some differences. According to the *South West Africa handbook* (1971-2), Swakopmund has an average yearly precipitation of 16.2 mm over 40 years of records; heavy rains

Figs 2-7.

Habitats of *Chamaeleo namaquensis*. Leeu-Gamka, Cape Province is also a habitat of *C. pumilus*. All other photographs were taken in South West Africa.

Fig. 2A.

The Karoo in the region of Leeu-Gamka, Cape Province, Republic of South Africa.

Fig. 2B.

Scattered thorn trees on grassland of South African Plateau in vicinity of Rehoboth.

Fig. 3A.

Outcropping of white weathered marble and black dolerite, Zwartbank Mountain, breaks featureless gravel plain of Namib Outer Platform.

Fig. 3B.

Base of large, red inland dune near Gobabeb, showing heavily overgrazed *Aristida sabulicola* hummock in right foreground. Hummock in left centre is a 'narras' (*Acanthosicyos horrida*).

Fig. 4A.

Kuiseb River bottoms with *Eragrostis spinosa* grass and *Acacia giraffae* and *A. albida* trees in the background. Large dunes form backdrop.

Fig. 4B.

Mud-cracked channel in stream-deposited gravel flats of the Swakop River. In the right centre is a *Chamaeleo namaquensis*. Nasal salt exudate appears as a small white spot on the chamaeleon's nose.

Fig. 5A.

Namib littoral at mouth of Swakop River, showing deposits of tidal wrack and other debris. *C. namaquensis* forages seawards at least to the tidal wrack.

Fig. 5B.

Featureless gravel plain near Swakopmund forming a street between dunes. Small *Zygophyllum stapffii* bush just visible at foot of dunes at right.

Fig. 6A.

Near Swakopmund, vegetationless coastal dune, on lee slope (slip-face) of which a chamaeleon was discovered with body temperature of 34.2°C (sand surface temperature, 67.0°C).

Fig. 6B.

Limestone outcrop on north bank of Swakop River, showing its barren flat-top. Small black dots are plants.

Fig. 7A.

River hummocks in bottomlands of Swakop River. Note inter-connected nature and larger size of this hummock type. *Eragrostis spinosa* grass forms partial cover.

Fig. 7B.

Dune hummock region. Predominant hummock vegetation is *Eragrostis spinosa* grass, *Trianthema* sp. and *Zygophyllum stapffii*. A single *Nicotiana glauca* is in right foreground; *Tamarix austro-africana* in left background on foot of dune, and a 'narras' (*Acanthosicyos horrida*) on foot of dune in distant left centre.



Fig. 2A.



Fig. 2B.



Fig. 3A.



Fig. 3B.



Fig. 4A.



Fig. 4B.



Fig. 5A.



Fig. 5B.



Fig. 6A.



Fig. 6B.



Fig. 7A.



Fig. 7B.

of 42,1 mm fell in 1969, with 41,3 mm falling in March alone, and as little as 0,4 mm in 1959. The Namib Desert has very little rain of erratic distribution, the causes of which are reviewed by Logan (1960) and Meigs (1966). Inland areas are both wetter (more rain) and drier (lower humidity) than coastal locales. Fog is a persistent and normal feature of the Namib Desert, especially along the coast, but its effect reaches far inland (at least 200 days per year, 58 km from the coast). The moisture realized from fog far exceeds that from rain, as demonstrated by Walter (1937), who in one month collected more than 250 litres of water condensed from fog on the inclined roof (60 m² in area) of a house in Swakopmund. The immense, similarly inclined plane of a dune must collect far more water, and percolation down and outward at the base explains the richer vegetation of inland dunes.

Table 2

Weather data for coastal and inland locales of the central Namib Desert. Temperatures are in degrees Celsius. Means in parentheses.

Location and month	Air at 2 m	Substrate temperatures			
		Surface		At 50 mm depth	
		Dune sand	Gravel	Dune sand	Gravel
1969					
Coastal	14,7-27,0	19,0-55,0	18,4-47,0	18,7-56,0	19,0-48,0
April.	(19,1)	(30,0)	(24,5)	(33,4)	(26,8)
Inland	7,0-38,0	8,0-48,5	8,0-46,0	9,0-50,0	8,0-47,0
April.	(25,5)	(31,5)	(25,6)	(28,5)	(27,2)
Coastal	6,0-35,0	8,0-35,0	8,5-33,0	8,0-35,0	9,0-33,0
June	(15,0)	(27,5)	(20,0)	(21,8)	(20,0)
Inland	4,0-35,0	6,0-38,5	5,5-36,5	6,6-43,0	6,3-42,0
June	(19,9)	(25,5)	(23,7)	(27,6)	(26,8)
Coastal	16,1-25,5	17,4-48,0	16,2-43,0	17,0-42,3	17,5-42,5
November	(19,9)	(33,1)	(30,3)	(34,3)	(31,3)
Inland	12,0-36,5	20,0-52,0	21,0-49,0	25,7-49,0	21,0-50,0
November	(24,4)	(37,3)	(30,6)	(36,7)	(32,7)
1970					
Coastal	16,8-34,0	19,9-67,0	19,7-45,0	20,3-70,0	19,5-45,0
February	(23,1)	(36,6)	(31,5)	(39,6)	(31,1)
Inland	10,3-42,5	14,0-83,0	14,0-80,0	14,0-85,0	14,0-83,0
February	(26,6)	(43,7)	(40,0)	(45,0)	(43,3)
\bar{x} Coastal	19,3	31,8	26,6	32,3	27,3
\bar{x} Inland	24,1	34,5	30,0	34,7	32,5

Data from personal records and the official records of the Namib Desert Research Station.

The daily fog regimen is well discussed by Logan (1960). Fog may be low or medium altitude, but drizzly ground fogs are frequent. Fog generally clears by mid-morning between 10:00 and 12:00 hours, returning by 15:00 hours, but varying with the time of the year, since in winter the sun is weaker and less vigorous in dissipating or preventing the return of fog. Indeed, some days the fog persists throughout. Another oddity is that maximum yearly temperatures along the coast coincide with the occurrence of the east wind in midwinter

(Logan 1960; Meigs 1966). In 1969 a June east wind gave a maximum of 33,9 C and in July 33,6 C, though winter 1969 was cooler and drier than normal. In January 1970 a midsummer maximum of 27 C was recorded, with no east wind condition. Logan considers east winds of rare occurrence. Winter minimums along the coast are to 6 C in June and July, about twice that in midsummer. Low maximum temperatures under fog were 11,4 C in July; 18,4 C in December; the corresponding lows for these days were 9,5 C and 14,5 C respectively, demonstrating the temperature insulating effect of fog. There is less temperature range in summer than in winter, though conditions do not vary greatly along the coast. The greatest temperature range is in winter with an east wind condition.

In summer, coastal winds are mostly northerly or north-westerly, often accompanied with drizzle when from the latter direction. Winter winds are southerly or south-westerly. Humidity is closely related to temperature, presence of fog and proximity to the Atlantic, being at or near 100% with low temperatures and fog. Near the coast humidity rarely falls below 90% even in the absence of fog cover. East winds drop humidity to 30%. Duration of fog and degree of humidity is less even a short distance from the coast, such as Swakopmund airport 1,8 km from the Atlantic, and lessens still further inland. Walvis Bay, partly protected by Pelican Point from the effect of the ocean, has conditions similar to Swakopmund airport and far less fog than at the Swakopmund lighthouse.

Fog has an effect at Gobabeb, but usually burns off sooner and returns later than along the coast. Air temperature minimums are lower and maximums higher at Gobabeb than at Swakopmund (Table 2). Though humidities of 100% occur, usually coinciding with fog, humidity tends to be lower at Gobabeb and as low as 5% with east winds. Other weather conditions are essentially as described for coastal sites, and are fully discussed for Gobabeb by Schulze (1969) and generally discussed by Logan (1960), Koch (1961) and Meigs (1966).

There is no great difference in dune sand and gravel substrate temperatures, other than for locality of both (Table 2). On dunes proper a considerable variation was apparent as to site and time of temperature data collected. For example, lee faces were hottest until such situations were shaded, when the crest was hottest. On winter afternoons dune lee faces are shaded earlier in the day. Dune temperature data have been omitted in this study, but Louw & Holm (1972) discuss these in detail in their study of the ecology of *Aporosaura anchietae*. Chamaeleons did not purposely seek cooler or warmer substrates or situations, as Warburg (1964) reported for vipers and Burrage (1966) for utas. Chamaeleons sometimes sought wind-protected sites to the lee of small objects. Burrage (1966) found a tremendous difference in thermal and textural qualities of nearby substrates and a consequent effect on the overall ecology of utas. Namib dune sand and gravel have an unfavourable heating gradient, barely heating under overcast conditions, when the substrate temperature approximated that of the air at 50 mm. Under clear skies dune sand and gravel heated

rapidly to high levels, and cooled equally rapidly. Strong, sustained wind also depressed substrate surface temperatures. Because of this it is an advantage for *Chamaeleo namaquensis* that, thermally speaking, it is less dependent on the thermal qualities of the substrate than most reptiles. Schulze (1969) discusses the soil (gravel) thermal regimen at Gobabeb.

Logan (1960) and Koch (1961) give general consideration to Namib Desert flora, but Giess (1962, 1968) considers this in greater detail. Giess (1962) divided the Namib Desert flora into: (1) red dunes; (2) Kuiseb and Swakop Rivers; (3) Namib Flats north of the Kuiseb River stretching to the mountainous area of the Swakop Canyon and farther north from the Swakop River; (4) the mountains, such as Zwartbank, Vogelfelderberg, and isolated granitic koppies arising from the flats.

According to Giess (1968), coastal plants have a cushionlike shape due to wind and sand and assist in formation of small secondary dunes of varied height. Beach flora consists of *Psilocaulon salicornioides*, *Zygophyllum clavatum*, *Salsola aphylla* and occasional *S. nollothensis*. On the gravelly flats just inland of the strand are very scanty, widely scattered *Zygophyllum stapffii* and *Arthraura leubnitziae*. Because of salt or gypsum, large tracts of these flats are barren. Eleven kilometres north of Swakopmund near Wlotzka's Baken great diorite boulders and stones shelter a richer flora, with *Drosanthemum paxianum*, *Ruschia*, *Tetragonia arbusculoides* and lichens. Sufficient rainfall permits growth of annuals. The gypsum plains have a rich growth of colourful lichens.

In dune regions the 'narras' (*Acanthosicyos horrida*) gives a thorny refuge to pursued reptiles. A few narras plants were found on the northern extremity of dunes at Swakopmund, though it is commoner on Gobabeb dunes. Large tufts of *Aristida sabulicola* are terribly overgrazed near the Kuiseb River in the Gobabeb area. *Aristida sabulicola* normally form hummocks on dune bases, the usually unharmed grass reaching heights of 1.5 m. *Acacia giraffae* trees occur on dunes near the banks of the Kuiseb River. *Tamarix austro-africana* (3-5 m high) are the commonest trees on the low dunes bordering the Swakop River. Both trees are frequently in various stages of burial by the shifting dunes. There are clumps of *Trianthema* sp. on small dunes.

The Kuiseb River has a distinct riverine forest, with large stands of *Acacia giraffae* and some *Acacia albida*. *Tamarix austro-africana* also occurs, but is virtually the only tree in the Swakop River region investigated. Density, variety and size of trees increase upstream. The exotic *Nicotiana glauca* is very common in the Kuiseb and Swakop River beds and bottomlands. *Salvadora persica* thickets line the banks of the Kuiseb River. Grasses consist of *Eragrostis spinosa*, singly or in thick stands, *Aristida sabulicola* (commoner in the Kuiseb River), and *Cynodon dactylon* and *Odysea paucinervis* are found in damper spots. In the Swakop River *Trianthema* sp. occurs singly in clumps or forms low, broad-based hummocks, resembling hummocks formed by *Cynodon dactylon*. After floods and rains, a variety of annuals and especially pretty flowers appears in these areas.

The Namib Flats, or gravel plains, are practically devoid of vegetation along the coast and for approximately 12–18 km inland. About the only vegetation are sparsely scattered *Zygophyllum stapffii* (0,25–0,5 m high), and *Arthraerua leubnitziae*, occasionally forming small hummocks. *Zygophyllum stapffii* is the only large plant on the barren limestone outcrop on the north bank of the Swakop River. Aizoaceae occur in the watercourses along with *Z. stapffii*. Lichens are also present. *Welwitschia* occurs in this biotope. Farther inland appear shrubs such as *Sutera canescens*, *Citrullus eccirhosus*, the very small *Acacia reficiens*, *Asclepias filiformis*, and the larger *Parkinsonia africana*.

The mountains have a richer vegetation, especially of succulents, due to greater moisture from fog condensing on stones. Four succulents, one herbaceous Euphorbia, and an *Aloe* are recorded by Giess (1962). Lichens are also very abundant.

Mertens (1955) gives an excellent review of the reptilian co-inhabitants of *Chamaeleo namaquensis*. No information is available on the reptiles that directly compete with *C. namaquensis*, but the larger species of the lacertid genus *Meroles* do eat mainly tenebrionid beetles, which also form the bulk of the chamaeleon's diet. However, there is no information that either lizard eats exactly the same species of tenebrionids, and selection of different tenebrionid species by each lizard may not place them in too great a degree of competition with each other for this food. *Chamaeleo namaquensis* is the more ubiquitous saurian, while most *Meroles* species are restricted to sandy situations. Where *Meroles* and *Chamaeleo* co-inhabit, the lacertid is the more numerous. But greater population density of the lacertid does not necessarily mean it is the more successful saurian. The lower population density of the chamaeleon may be due to factors other than competition between these saurians. Furthermore, the population density of *C. namaquensis* does not greatly vary in all the diverse habitats in which it is found.

It seems that smaller reptiles chanced upon by *Chamaeleo namaquensis* are potential prey for it; the larger reptiles, potential predators of it. The only lizard that could prey on *C. namaquensis* is *Varanus*, which occasionally ventures from the Great Western Escarpment along the rivers into the barren desert. *Chamaeleo namaquensis* lives in the *Salvadora persica* thickets, which are also frequented by large cobras (*Naja*). *Bitis caudalis* may prey on *C. namaquensis*. Smaller snakes, saurians and sometimes geckos (*Rhoptropus*), are eaten by *C. namaquensis*. The nocturnal geckos, for example, *Ptenopus* and *Palmatogecko*, should be safe from *Chamaeleo namaquensis* because of their habits. *Palmatogecko* tracks were observed on the dune sand skirt of the limestone outcrop on the north bank of the Swakop River.

E. Mortality

1. Parasitism and disease

Elkan (1965) describes a fungal infection, probably by *Candida albicans*, destroying one half of the liver of a *Chamaeleo bitaeniatius*. Another *C. bitaeniatius*

suffered a dermal fungal (Dematiaceae) infection. The reaction of the chamaeleon's skin was an increasing keratinization and thickening of the stratum germinativum, and ulceration of the dermis which contains the melanophores. This condition would prevent colour lability, disrupting chamaeleon thermoregulation and result in loss of appetite, general weakened condition and eventually death. An ailment affecting thermoregulation of *Chamaeleo namaquensis* and *C. pumilus* is discussed later under thermoregulation (see p. 55). It is not known what etiological agent was involved. These afflicted chamaeleons were unable to turn darker shades, and hence had trouble in warming at cool experimental temperatures. They had no difficulty in keeping cool at high experimental temperatures. Disruption of physiological thermoregulatory capacity greatly lowered the high metabolic rate of chamaeleons, resulting in loss of appetite, increasing listlessness, daytime sleeping, and eventual death.

Culex mosquitoes were observed feeding on *Chamaeleo namaquensis* at Gobabeb, South West Africa. Brygoo, Dodin & Sureau (1959) report *Culex fatigans* feeding on *Chamaeleo lateralis* and *C. verrucosus* of Madagascar. No other ectoparasites were observed on *Chamaeleo namaquensis* or *C. pumilus*. Brygoo and his associates have worked on the many protozoan parasites of Madagascan chamaeleons. Microscopic parasites were not examined in either *Chamaeleo pumilus* or *C. namaquensis*, but macroscopic endoparasites, which were encountered during autopsies of chamaeleons in association with investigations of diet, and reproduction, were removed. Dr Prudhoe of the British Museum (Natural History) kindly identified such parasites, and published his findings separately (Prudhoe & Harris 1971).

In January 100% of female *Chamaeleo pumilus* harboured intestinal parasites, but in October only 14.2% were so parasitised. In January, February, July and October 100% of male *C. pumilus* had intestinal parasites, but this incidence was only 16.7% in June. The greatest number of parasites was 70 nematodes removed from a female *C. pumilus*, whereas 36 was the largest number of nematodes removed from a male. In June a female *C. pumilus* weighing 15.4 g had a total parasite complement of 1.2 g consisting of 23 nematodes and 7 cysts variously on the bladder, ovaries and in the abdominal wall. It seemed healthy and yolking of follicles appeared normal. In April and August every *C. namaquensis* examined contained some parasites, but in June only 50% were parasitised. Intestinal parasites were mostly tapeworms in this species, with some nematodes, acanthocephalans and small cysts in the body wall.

According to Dr Prudhoe, the nematodes in *Chamaeleo pumilus* were all *Strongyluris*, but all the cysts were undergoing calcification, making them impossible to identify. However, one cyst showed great superficial resemblance to a cestode cysticercous. The cestodes of *C. namaquensis* were all *Oochoristica africana*, the nematodes *Physaloptera* sp., and the acanthocephalan larvae possibly of the genus *Echinopardalis*, which occurs as adults in mammalian carnivores. *Oochoristica africana* also occurs in the saurians *Agama* and *Meroles*. The cysts found in *Chamaeleo namaquensis* had also undergone calcification to a

degree making accurate identification impossible. Helminths, covered by a gelatinous covering, were frequently observed among tenebrionid beetle remains in the stomachs of *C. namaquensis*. Chabaud & Brygoo (1960) and Brygoo (1963) record nematodes and trematodes of Madagascan chamaeleons, only the nematode *Strongyluris* being represented in their and this study's samples.

2. Predation

No actual field predation on *Chamaeleo pumilus* or *C. namaquensis* was observed. Defence is discussed later under that section in behaviour (see p. 73). While *C. pumilus* females are alleged (Rose 1950) to devour their young, this was found to be accidental, and triggered by a fruit-fly landing on or near the baby. Captured babies were not eaten, though usually killed by such mistaken identity on the part of the adults. A *C. dilepis* in captivity did eat young *C. pumilus*, and its presence caused some upset among the adults. Snakes of the genera *Dendroaspis*, *Dispholidus*, *Philothamnus* and *Thelotornis* are recorded (FitzSimons 1962) as predators on chamaeleons. According to Dr R. Jensen of Gobabeb, the raptorial birds *Falco rupicoloides*, *F. terinunculus* and *Melierax musicus*, and the mammal *Canis mesomelas*, prey on *Chamaeleo namaquensis*. Rose (1950) says shrikes eat *C. pumilus*, and, indeed, one can see the catch stored on barbed wire fences. Wager (1958) records cats, dogs, motor traffic, raptorial birds and snakes as mortality factors of *C. dilepis*, and also a spider ensnaring a young individual. Cats and dogs, particularly the former, preyed on *C. pumilus*, and the feral dogs of the Walvis Bay vicinity may prey on *C. namaquensis*. Chamaeleons sustained severe injuries, often fatal, as the result of intraspecific action (see under population structure, social interactions, p. 101).

3. Physical

Wager (1958) considers grassfires cause 'many thousands' of chamaeleon deaths. Fortunately, or unfortunately, none of the marked chamaeleon populations examined suffered any fires during the study period, so the real effect of this mortality factor cannot be estimated. Fire-ravaged grassy areas were combed, where previously *Chamaeleo pumilus* had been observed, but no remains were uncovered. *C. pumilus* at such sites appeared unscathed by such fires, provided they climbed high enough into tall reeds which were moist enough to resist burning, or evacuated to such nearby. It is not known whether chamaeleons found in burnt areas were simply returning refugees originally located there, or new individuals. Fire was scarcely a problem to *C. namaquensis*, since any burning of the meagre and scant vegetation of their habitat would be most local and easy to escape.

Fire is 'normal' in areas of scant or seasonal rainfall. Burrage (1966) feels that fire is beneficial to reptiles preferring open spaces, since fire clears dense growth that crowds such reptiles out. Fire would be beneficial to *Chamaeleo pumilus* in limiting tall trees from crowding out the bushes and grasses which it prefers, and which rapidly recover in burned areas.

No instance of flooding deaths in *Chamaeleo pumilus* is known, but any sudden, large increase in river volume would be suspected to have deadly effect on chamaeleons inhabiting stream-side vegetation. Flooding may be a mortality factor of those *C. namaquensis* directly inhabiting water courses in narrow canyons and bottom lands of intermittent rivers subject to sudden and erratic discharge. This would necessarily depend on the discharge at any given time of a given stream and the topography in the immediate area.

Burrage (1966) reports flooding of washes caused as high as 95% mortality of *Uta stansburiana hesperis* inhabiting such situations, though the effect on the overall population was minor. Those *U. s. hesperis* inhabiting a burn area of 2 050 m² suffered a 33.3% mortality.

Rand (1968) reports suffocation in nest-building *Iguana* of Panama, when their excavations collapsed and they could not free themselves. In captivity a male *Chamaeleo namaquensis* was rescued and survived a cave-in of its retreat burrow, but a female of this species died when its nest burrow collapsed.

4. Human agency

Setting of fires, spraying with insecticides, alteration of habitat, capture and killing for any of several reasons by man must rate as predation, since an animal permanently removed from a specific locality is denied to that local population as surely as if it had been killed and eaten. Alteration of the habitat is probably man's most destructive effort, because it totally eliminates a habitat and all forms dependent upon it. It was felt at Gobabeb that *Chamaeleo namaquensis* was rare there owing to the Kuiseb flooding in 1969. This is very much doubted. They were very much in evidence elsewhere along and in the Kuiseb away from Gobabeb, and flooding could not be a mortality factor on the gravel plains and dunes in the immediate Gobabeb area. Moreover, they were common in other riverbeds that were also subject to flooding at the same time as the Kuiseb.

Survival of *Chamaeleo pumilus* and *C. namaquensis* is discussed in the section on population structure (see p. 95).

F. Temperatures and their control: activity patterns

1. Regulation of temperatures

Most reptiles are considered ectotherms, though Benedict (1932), Templeton (1960), Dawson & Templeton (1963), Bartholomew & Tucker (1963), Norris (1967), Dawson (1967) and Weathers (1970) have shown that a number of forms supplement behavioural thermoregulation with purely physiological mechanisms. Ectotherms acquire and lose body heat by: (1) radiation; (2) conduction, primarily with the substrate; (3) air convection. Although at extremely high temperatures some lizards pant, this may be a wasteful recourse in the case of deserticulous species. Many diurnal forms maintain their body temperatures within narrow limits by behavioural adjustments, as demonstrated by Cowles & Bogert (1944).

Diurnal deserticulous lizards apparently have the most varied means of controlling their temperatures, employing physiological methods to increase their activity time beyond the restrictions of behavioural thermoregulation and in 'hostile' thermal conditions. This is discussed by Dawson (1967), Tucker (1967) and Mayhew (1968), who point out the following methods: (1) toleration of hyperthermia; (2) changes in surface-volume ratio by body expansion and contraction; (3) changes in reflectivity; (4) changes in the cardiovascular system affecting heat transport through the tissues. Richards (1970) discusses the use of evaporative cooling by reptiles.

2. Thermal preferences in the field

Chamaeleo pumilus is active even on rainy winter days that would seemingly deter any heliothermic reptile. It is able to be abroad because it is eurythermic and partly endothermic. Of 549 active *C. pumilus* body temperatures recorded, the overall yearly range was 3,5–37,0 °C (\bar{x} = 22,4 °C; median 22,8 °C). These data are given by season and weather condition in Table 17, and summarized in Table 3. Body temperatures differed according to season and weather conditions (Table 17). Seasonal differences have been reported in American iguanids by Tinkle (1967) for *Uta stansburiana* and McGinnis (1966) for *Sceloporus occidentalis*.

Fifteen records of low active body temperatures (3,5–9,9 °C) for *Chamaeleo pumilus* were all taken under 'Cool Fair' conditions. Two *C. pumilus* with body temperatures of 3,5 °C were catching flying prey. All these low readings,

Table 3

Environmental temperatures (°C) related to body temperatures (°C) and activity states of 603 *Chamaeleo pumilus* at Stellenbosch, Cape Province.

Environmental temperatures (Mean in parentheses)	Body temperatures	State and number of individuals		
		Basking Cool/Warm	Foraging Open/Shade	Retreat
32,0–39,0 (34,9)	36,0–37,9		4 6	
27,0–39,0 (32,7)	34,0–35,9		7 10	
27,0–35,0 (31,2)	32,0–33,9		17 15	
20,7–31,8 (28,3)	30,0–31,9		17 13	
19,0–32,5 (24,7)	28,0–29,9		27 4	
18,4–31,0 (21,7)	26,0–27,9	5	46 5	4
14,5–24,5 (20,0)	24,0–25,9	6	70 10	1
14,5–22,0 (18,8)	22,0–23,9	10	75 1	5
13,0–21,5 (17,1)	20,0–21,9	10	30	2
13,0–20,1 (17,8)	18,0–19,9	6	25 9	5
6,5–17,2 (14,5)	16,0–17,9	7	12 4	2
12,0–15,2 (13,8)	14,0–15,9	4	10	2
9,0–13,2 (11,6)	12,0–13,9	7	2	3
11,0–11,6 (11,3)	10,0–11,9	2	1	7
9,3–11,4 (10,6)	8,0– 9,9	2	4	6
5,0– 7,2 (6,1)	6,0– 7,9	5	3	3
3,6– 5,0 (4,5)	4,0– 5,9	1	5	5
2,0	2,0– 3,9		3	4
0,0– 1,7 (0,5)	0,0– 1,9			5

Numbers do not quite add up to 603, since some individuals were engaged in several activity states simultaneously.

however, were taken very early in the day (mostly before 08:00 hours), about 15 minutes before sunrise. These low body temperatures of active *C. pumilus* in the field agree with the body temperatures of 40,0 C recorded by Pearson (1954) for the Andean iguanid *Liolaemus multiformis*. Records for 45 *Chamaeleo pumilus* asleep and mostly taken at night range from 0,5 C ('Cool Fair') to 26,5 C ('Warm Fair'), and were almost the same as that of the air temperature at 50 mm (= Environmental Temperature). Body temperatures for active *C. pumilus* and for those at rest were monitored on a 24-hour basis. Table 6 gives a summary of body temperatures of selected lizards active in nature, which are co-inhabitants, or of similar habits as *C. pumilus* and *C. namaquensis*, the relevance of which is discussed later. These data are taken from Brattstrom (1965), though recent data have been included. Where the incorporation of new data differs from those of Brattstrom, the newer source has been credited.

Chamaeleo pumilus dies if held at $-5,0$ C for a minimum of two hours, and this temperature is considered the minimum lethal temperature. Though torpor does occur at this temperature, *pumilus* does react to pinching and prodding at 0,0 C and even $-5,0$ C for a time. The critical maximum temperature is 43,0 C; the maximum lethal temperature 43,0–47,0 C.

The body temperatures of active *Chamaeleo namaquensis* are remarkably stable, despite the varied environmental temperatures of the Namib Desert. On foggy mornings the substrate temperature was as low as 8,0 C; but on clear, sunny days the substrate temperature reached 67,0 C. Of 351 active *C. namaquensis* body temperatures recorded in the field, the overall range was 14,0–39,7 C; mean 28,7 C; median 28,8 C (Coastal, 14,0–36,2 C; $\bar{x} = 27,0$ C; median 28,4 C; Inland, 15,0–39,7 C; $\bar{x} = 30,3$ C; median 31,5 C). These data treated seasonally, are given in Table 17, and summarized in Tables 4 and 5. There is slight difference in weather and season in the means and between coastal and inland populations, but it is not significant. Though body temperatures of inland *C. namaquensis* were slightly higher, the range of body temperatures is about the same for the respective populations, regardless of weather conditions.

Most diurnal desert lizards have far higher mean body temperatures than *C. namaquensis* (Table 6) and this is discussed in the section on thermoregulation (see p. 37). *C. namaquensis* not only has the normal desertic problem of adaptation to and survival of high environmental temperatures, but also one of tolerating low environmental temperatures, or controlling its body temperature by physiological means. It solves its thermal needs to both environmental extremes by recourse to the latter solution. *C. namaquensis* shows discomfort at a body temperature of 41,0 C; is 'troubled' (seeks shade, mouth gaping, eye bulging) at 45,0 C; its critical thermal maximum was 47,0–48,0 C and lethal temperature was 49,5 C $\pm 1,3$. There was no difference in critical thermal maximum between inland and coastal individuals. The critical minimum temperature was 0,0 C for two hours; the minimum lethal temperature, $-5,0$ C for a minimum of two hours. Partial torpor occurred at a body temperature of 13,5 C (coastal), 15,5 C (inland), though pinching evoked response

Table 4

Environmental temperatures (°C) related to body temperatures (°C) and activity states of 272 coastal *Chamaeleo namaquensis* in South West Africa.

Environmental temperatures (Mean in parentheses)	Body temperatures	State and number of individuals		
		Basking Cool/Warm	Foraging Open/Shade	Retreat
50,0-58,0 (55,0)	36,0-37,9	3	6	
67,0	34,0-35,9		1	
25,5-47,5 (36,0)	32,0-33,9	14	14	
20,5-45,0 (31,0)	30,0-31,9	20	10	6
21,5-38,0 (25,5)	28,0-29,9	10	22	2
18,2-47,0 (29,5)	26,0-27,9	29	33	6
14,7-30,7 (21,4)	24,0-25,9	12	15	4
20,4	22,0-23,9	10	16	8
14,7-19,5 (17,1)	20,0-21,9	4	4	4
16,5-19,5 (18,0)	18,0-19,9	4	2	2
14,0-17,0 (15,5)	16,0-17,9	2	2	2
8,0-16,0 (11,6)	14,0-15,9	4	4	6

Numbers do not add up to 272, since some individuals were engaged in several activity states simultaneously.

Table 5

Environmental temperatures (°C) related to body temperatures (°C) and activity states of 97 inland *Chamaeleo namaquensis* in South West Africa.

Environmental temperatures (Mean in parentheses)	Body temperature	State and number of individuals		
		Basking Cool/Warm	Foraging Open/Shade	Retreat
48,5-58,0 (53,3)	38,0-39,9		5	
37,0-48,5 (41,5)	36,0-37,9		10	3
34,0-40,0 (37,1)	34,0-35,9	4	8	
32,6-38,5 (35,6)	32,0-33,9		6	3
30,0-43,5 (40,7)	30,0-31,9	8	29	6
32,0-34,0 (33,3)	28,0-29,9			
30,0-36,0 (33,0)	26,0-27,9	4	8	
23,0	24,0-25,9	2		
—	22,0-23,9			
—	20,0-21,9			
—	18,0-19,9			
12,5	16,0-17,9	2		5
—	14,0-15,9			

Numbers do not quite add up to 97, since some individuals were engaged in several activity states simultaneously.

down to a body temperature of 10,0 C. Full torpor occurred at a body temperature of 7,6 C.

Field records (N = 18) of *C. namaquensis* at rest ranged from (coastal N = 11) 7,0-13,0 C (\bar{x} = 10,6 C), and (inland N = 7) 9,0-16,0 C (\bar{x} = 12,3 C) and were about that of the substrate.

3. Thermal preferences in the laboratory

In a laboratory thermal gradient active *Chamaeleo pumilus* body temperatures (N = 20) ranged from 7,0-30,0 C (\bar{x} = 25,0 C), which is the ambient preferendum Von Frisch (1962) found. Bustard (1963) kept his *C. pumilus* at

30,6 C during the day. Laboratory resting temperatures (15,0–25,0 C; \bar{x} = 22,0 C) are similar to 'Warm Fair' field records, thus *C. pumilus* 'prefers' a higher resting (= nocturnal) environmental temperature, if it is available.

Like Von Frisch, Bustard (1965) did not take actual body temperatures, but records 36 captive *Chamaeleo hohnelii* active at an ambient temperature of 2,0–3,0 C and catching food at 10,0 C. Bustard (1966) also observes *C. bitaeniatus* is quite hardy, surviving ambient nocturnal temperatures of 36–39 F (2,0–4,0 C). Unlike *C. pumilus*, *bitaeniatus* and *hohnelii* of East Africa inhabit montane grasslands.

Chamaeleo namaquensis (N = 18) active preferred body temperatures ranged from 18,5–36,2 C (\bar{x} = 29,3 C), with no difference between inland or coastal individuals. The eccritic range was somewhat wider (14,0–39,7 C) but the mean (28,7 C) of both populations was close to laboratory findings. Stebbins (1961) gives a preferred body temperature range of 28,5–36,5 C (\bar{x} = 33,5 C) based on 27 records of two captive *C. namaquensis*. Greatest similarity in eccritic and preferred body temperatures is that for 'Warm Overcast' (coast 17,5–35,4 C; \bar{x} = 27,7 C; inland 20,0–39,0 C; \bar{x} = 29,0 C). The eccritic body temperatures of both populations do not differ considerably with most seasonal and weather conditions. Resting laboratory *C. namaquensis* body temperatures (25,0–29,7 C; \bar{x} = 28,7 C) were not really different from active preferred body temperatures, thus *C. namaquensis*, as *C. pumilus*, prefers warmer resting temperatures, if available. At night they did not select lower resting temperatures available, as Regal (1967) reported for some of his desert lizards.

As Mayhew (1968) points out, the eccritic and preferred body temperatures may be essentially the same for some species, but it is not the rule (Licht *et al.* 1966a, b). DeWitt (1963, 1967) found the deserticolous iguanid *Dipsosaurus dorsalis* to have a mean preferred body temperature of 38,5 C, whereas 42,1 C was the mean eccritic body temperature (Norris 1953). It is difficult to simulate in the laboratory the various weather conditions, such as rain, cloud, fog, and wind to which reptiles are subjected in the field. Thus, even if within the environmental range it is considered that laboratory thermal gradients do not give a clear reflection of the actual thermal factors of the environment, the thermal preferences of reptiles, or their need, ability, or lack of it to make thermoregulatory adjustments. This study agrees with Bustard (1967b), who thought that any difference in active preferred and eccritic body temperatures indicates that optimum temperatures exist for different functions. Artificially supplied temperatures also allow selection of, rather than regulation to, the preferred body temperature, without the variabilities imposed on it by other environmental factors.

4. Thermal preferences of chamaeleons in comparison with other saurians

The thermal preferences of co-inhabitants of, and species of similar habitat and habits as *Chamaeleo pumilus* and *C. namaquensis* are summarized in Table 6. Body temperatures of *C. pumilus* have a range similar to those of the Andean

Table 6

Summary of body temperatures (°C) of selected lizards active in nature, co-inhabitants of or of similar habits as *Chamaeleo pumilus* and *C. namaquensis*.

Species	Range	\bar{x}	min. Crit.	max. Crit.	N	Ref.
AGAMIDAE						
<i>Agama atra</i>	29,0-32,0	30,5			20	5
<i>Amphibolurus barbatus</i>	25,2-40,0	33,8			94	9
„ <i>caudicinctus</i>	34,8-41,0	39,0			15	9, 10
„ <i>inermis</i>	34,5-43,0	39,3			47	10
„ <i>reticulatus</i>	35,0-40,6	37,0			6	10
<i>Physignathus longirostris</i>	34,2-39,0	37,0			26	10
<i>Moloch horridus</i>	27,2-40,2	33,7			88	9, 14
CHAMAELEONIDAE						
<i>Chamaeleo dilepis</i>	21,0-36,5	31,2			328	15
„ <i>namaquensis</i> (coast)	14,0-36,2	27,0			261	7
„ „ (inland)	15,0-39,7	30,3	0,0	47,0-48,0	90	7
„ <i>pumilus</i>	3,5-37,0	22,4	-5,0	43,0	549	7
GEKKONIDAE						
<i>Rhoptropus afer</i> (coast)	19,0-38,0	28,0			550	5
„ „ (inland)	28,5-36,5	32,7			12	4
HELODERMATIDAE						
<i>Heloderma suspectum</i>	24,2-33,7	27,2			>57	
„ <i>horridum</i>	25,6-36,0	28,7			5	5
IGUANIDAE						
<i>Anolis allisoni</i>	28,2-36,6	33,0			122	
„ <i>allogus</i>	26,2-33,5	29,2			148	
„ <i>carolinensis</i>	18,0-37,5	27,0		41,8	25	5
„ <i>homolechis</i>	26,2-35,0	31,8			104	
„ <i>limifrons</i>	24,6-31,0	27,1			761	1
„ <i>lucius</i>	24,8-32,4	29,3			86	
„ <i>sagrei</i>	27,4-36,1	33,1			178	
<i>Basiliscus vittatus</i>	22,5-38,5	35,0		41,0-44,6	720	
„ <i>plumifrons</i>	28,0-35,5	31,7			20	
<i>Callisaurus draconoides</i>	26,4-40,2	38,0	-3,0		>17	
<i>Crotaphytus collaris</i>	20,7-43,3	37,2	-2,0	46,5	>425	
„ <i>wislizeni</i>	23,0-41,4	38,3			>19	
<i>Dipsosaurus dorsalis</i>	27,0-47,0	40,0	0,0	47,5	many	
<i>Holbrookia texana</i>	32,0-40,2	37,1			6	
<i>Iguana iguana</i>	26,7-42,4	33,3		46,7	>37	
<i>Liolaemus multiformis</i>	4,0-37,0	35,0			?20	13
<i>Phrynosoma coronatum</i>	20,8-39,0	34,9	-3,0	46,7	>28	
„ <i>platyrhinos</i>	26,2-39,5	36,0		45,5	many	
„ <i>m'calli</i>	29,3-41,0	37,4			19	
<i>Sator grandaevus</i>	32,6-38,8	35,7			35	
<i>Sauromalus obesus</i>	23,8-42,0	37,9		45,6	many	
<i>Sceloporus gracilis</i>	30,3-39,1	33,6			38	
„ <i>graciosus</i>	20,8-38,2	34,2			101	
„ <i>jarrovi</i>	32,2-37,0	35,0			15	
„ <i>magister</i>	31,0-37,0	34,8	-3,0	43,0	many	
„ <i>merriami</i>	29,6-37,4	33,6			11	
„ <i>occidentalis</i>	26,4-38,0	35,0	-3,0	44,0-46,8	>500	
„ <i>orcutti</i>	26,0-38,5	35,4			21	
„ <i>poinsetti</i>	30,8-38,4	34,2			20	
„ <i>squamosus</i>	32,5-38,0	35,3			13	
„ <i>undulatus</i>	25,0-38,9	34,8		43,7	>54	
„ <i>variabilis</i>	33,1-40,0	34,1		43,0	110	
„ <i>woodi</i>	32,0-39,2	36,2		44,2	42	

Table 6 continued

Species	Range	\bar{x}	min. Crit.	max. Crit.	N	Ref.
<i>Uma notata</i>	18,0-46,0	39,8			>529	12
„ <i>scoparia</i>	26,6-39,0	35,7			13	
<i>Urosaurus auriculatus</i>	32,3-39,0	36,3		43,5	25	
„ <i>clarionensis</i>	29,6-39,0	36,4		41,8	59	
„ <i>nigricaudus</i>	33,8-39,5	36,2			14	
„ <i>ornatus</i>	26,8-39,5	35,5		43,1	97	
<i>Uta stansburiana hesperis</i>	17,2-40,6	34,1			404	6
„ „ <i>stejnegeri</i>	25,0-37,8	35,6			50	6
„ <i>thalassina</i>	32,6-38,8	35,6			22	
LACERTIDAE						
<i>Aporosaura anchietae</i> (coast)	26,0-42,0	34,0			100	5
„ „ (inland)	26,4-38,3	32,4		45,1	13	4, 11
<i>Eremias lineo-ocellata</i>	35,0-41,5	38,4			16	
„ <i>namaquensis</i> (coast)	19,0-36,0	27,0			777	5
„ „ (inland)	36,0-40,0	38,5			10	4
<i>Meroles cuneirostris</i>	24,2-39,1	35,0		45,4	24	4
„ <i>namaquensis</i>	36,0-40,0	38,5			10	
„ <i>reticulata</i> (coast)	19,0-36,0	27,0			852	5
„ „ (inland)	25,0-43,0	38,6			111	5
„ <i>suborbitalis</i>	36,0-41,5	38,8		44,0	18	
SCINCIDAE						
<i>Eumeces fasciatus</i>	13,5-37,0	33,0	-2,5		41	
„ <i>obsoletus</i>	17,5-36,3	34,0			39	
<i>Lygosoma laterale</i>	22,0-35,5	28,8			16	
<i>Mabuya capensis</i>	19,0-40,0	27,7			676	5
„ <i>occidentalis</i>	19,0-37,0	26,0			901	5
„ <i>striata</i>	31,0-39,5	35,8			121	
„ <i>multifasciata</i>	29,6-37,8	33,7			12	
„ <i>rudis</i>	25,4-38,6	32,8			31	
<i>Sphenomorphus sabanus</i>	24,0-28,4	25,8			16	
<i>Tiliqua occipitalis</i>	30,5-35,5	33,7			8	9
„ <i>rugosa</i>	25,0-41,0	34,6			125	9, 16
„ <i>scincoides</i>	29,5-39,5	34,9			9	2
TEIIDAE						
<i>Ameiva ameiva</i>	35,1-39,3	37,6		46,2	10	
„ <i>festiva</i>	32,0-39,8	36,2			70	
„ <i>quadrilineata</i>	24,0-42,0	37,6		45,1	698	
„ <i>pluvianota</i>	33,8-40,0	37,8			21	
<i>Cnemidophorus ceralbensis</i>	36,7-41,6	40,1			13	
„ <i>hyperythrus</i>	36,8-41,6	39,0			17	
„ <i>lemniscatus</i>	34,5-42,3	38,8			44	
„ <i>sexlineatus</i>	27,0-45,0	40,4			many	
„ <i>tigris</i>	29,0-44,6	40,4			>47	
VARANIDAE						
<i>Varanus</i> spp.*	20,0-40,0	36,0			12	3
„ <i>gouldii</i>	34,4-36,2	37,1			6	

* *acanthurus*, *gouldii*, *punctatus*.

Where uncredited, data shown are derived from Brattstrom (1965). Data for other species are identified by the following numbers to the references given below, as are the incorporation of new data for species listed by Brattstrom.

(1) Ballinger, R. E., K. R. Marion & O. J. Sexton (1970). (2) Bartholomew, G. A., V. A. Tucker & A. K. Lee (1965). (3) Bartholomew, G. A. & V. A. Tucker (1964). (4) Brain, C. K. (1962). (5) Burrage, B. R. (unpublished data). (6) Burrage, B. R. (1966). (7) this study. (8) Hirth, H. F. (1965). (9) Lee, A. K. & J. A. Badham (1963). (10) Licht, P., W. R. Dawson & V. H. Shoemaker (1966a). (11) Louw, G. N. & E. Holm (1972). (12) Mayhew, W. W. (1968). (13) Pearson, O. P. (1954). (14) Pianka, E. R. & H. D. Pianka (1970). (15) Stebbins, R. C. (1961). (16) Warburg, M. R. (1965).

iguanid *Liolaemus multiformis* and *Lacerta agilis* of the Russian Caucasian Mountains. *Lacerta agilis* maintains body temperatures 29,9 C above that of the environment (Strel'nikov 1944). Though their thermal problems are equivalent, the habitats of these three lizards are quite different, as *Liolaemus multiformis* and *Lacerta agilis* inhabit high mountains, while *Chamaeleo pumilus* does not encroach above lower mountain slopes. The montane chamaeleons, *C. bitaeniatus* and *hohnelii*, are 'active' in a similar thermal range in the laboratory, but for these species there are no field temperature data. These viviparous *Chamaeleo* may regulate to lower temperatures for reproductive reasons, which is discussed later in the section on reproduction. *C. pumilus* occurs sparsely in montane valleys and is subject there to lower environmental temperatures than those inhabiting lowlands.

The chief co-inhabitant of *C. pumilus* is the skink *Mabuya capensis*. *M. capensis* is active from 19,0–40,0 C (\bar{x} = 27,7 C), and is not abroad with body temperatures as low as *C. pumilus*, tolerates a body temperature slightly higher than the chamaeleon and has a higher mean body temperature. *Mabuya capensis* is rarely active in rainy weather, and usually keeps within dense vegetation avoiding exposure to the weather as does *Chamaeleo pumilus*. *Mabuya capensis* is chiefly a heliothermic skink, using dead vegetation as an insulator as does *Liolaemus multiformis* (Pearson 1954) and *Uta stansburiana* (Burrage 1966) to maintain very high body temperatures, much above that of the environment. How chamaeleons maintain higher or lower body temperatures compared to environmental temperatures is discussed in the thermoregulation—warming/cooling section (see p. 42). *Mabuya capensis* and *M. rudis* differ from most skinks in being active thermoregulators. *Agama atra* is another co-inhabitant of *Chamaeleo pumilus*. *Agama atra* is far commoner than the chamaeleon on mountain slopes; the reverse is true in lowlands. The agamids recorded (N = 20) had a body temperature range of 29,0–32,0 C (\bar{x} = 30,5 C).

The New World iguanid anoles (*Anolis*) are the ecological equivalents of the Old World chamaeleonids. *Chamaeleo pumilus* and *Anolis carolinensis* seem of quite similar habits and live under roughly comparable conditions. Most of the other species of *Anolis* listed in Table 6 are Neotropical, though some are mountain-dwelling, and others (e.g. *A. limifrons* and *A. frenatus*) inhabit closed canopy forests and are less warm-adapted than grassland or ecotone species, such as *A. auratus* and *A. tropidogaster* (Ballinger *et al.* 1970). Brattstrom's (1965) temperature data for *A. carolinensis* are for resting individuals, and those given in Table 6 are data collected by the author over several years from animals living in outdoor enclosures in New Jersey, Kansas and California. Thus, they are not 'field' body temperatures *per se*, but are all that are known of for this abundant species. The minimum voluntary body temperature (18,0 C) of active *Anolis carolinensis* is much higher than that of *Chamaeleo pumilus*, and the mean body temperature of *Anolis carolinensis* is slightly higher. However, the maximum voluntary body temperatures of both species are almost the same. *A. carolinensis* was also subject to approximately the same weather conditions,

thus environmental temperatures are about the same, and judging the range of *A. carolinensis* (south-eastern United States of America) the similarity of these species seems valid. *Basiliscus* and some *Sceloporus* are also forms of somewhat similar habitat and habits as *Chamaeleo pumilus*.

Body temperature data of four *Chamaeleo dilepis* were recorded in the field at Windhoek, South West Africa. Data for this species are within the range Stebbins (1961) gives for 328 records of 30 captives. *Rhoptropus afer* is a co-inhabitant of *Chamaeleo namaquensis*. Like the chamaeleonid, there is a difference in the ecritic thermal preferenda of the coastal and inland populations of this diurnal gekkonid (Table 6). *Rhoptropus* only emerges when it can maintain a minimum body temperature of 19.0 C. It was never seen abroad during completely overcast conditions, but was active on the hottest days. At both times *Chamaeleo namaquensis* was active. *Rhoptropus* has temperature preferenda similar to the co-inhabitant lacertids *Eremias namaquensis*, *Meroles reticulata*, and the scincid *Mabuya occidentalis*. The principally dune-dwelling lacertid *Aporosaura anchietae* has been studied in detail by Louw & Holm (1972). This study's records are for coastal individuals only and appear to be slightly different from those of Brain (1962) and Louw & Holm (1972). *Aporosaura* is similar in psammophilous adaptations and thermal requirements to the iguanid genus *Uma* of the deserts of the south-western United States of America. Other desertic saurians are: *Cnemidophorus* (teiid), *Tiliqua* (scincid), *Callisaurus*, *Crotaphytus*, *Dipsosaurus*, *Holbrookia*, *Phrynosoma*, *Sator*, *Sauromalus*, (most listed) *Sceloporus*, *Urosaurus*, *Uta* (iguanids), *Heloderma* (helodermatid), *Amphibolurus* and *Moloch* (agamids).

Chamaeleo namaquensis has a low minimum voluntary body temperature for a diurnal desert saurian and most other species have far higher maximum voluntary and mean body temperatures. The American deserticulous iguanid *Dipsosaurus dorsalis* and *Chamaeleo namaquensis* are active in the extreme midday desert heat at environmental temperatures lethal to most birds, and probably all mammals. *Dipsosaurus* is active with a body temperature of 47.0 C on substrates reaching 60.0 C. A *Chamaeleo namaquensis* active with a body temperature of 34.2 C was recorded on vegetationless dune sand with a temperature of 67.0 C, and five records gave maximum voluntary body temperatures of 39.7 C for *C. namaquensis* on substrates with temperatures of 48.5–58.0 C (\bar{x} = 53.3 C). Some of these chamaeleons were probably in transit between grass clumps, but others were in areas apparently devoid of any sort of available shade.

Gates (1970) contends that by knowing the properties of a particular species, one can predict the climate under which it must live. He has predicted the climatic parameters for *Dipsosaurus dorsalis*.

Iguanids, agamids and teiids are the most heat resistant lizards, skinks and xantusids are heat sensitive, while geckos vary in this regard according to species (Mayhew 1968). *Chamaeleo pumilus* is active over a broad span of body temperatures (34.5 C), but its critical minimum and critical maximum agree closely with such thermophilic deserticulous forms as *Callisaurus* and *Sceloporus*

(iguanids), which are not as low as the heat sensitive skink, *Eumeces fasciatus*. *Chamaeleo namaquensis* has the same critical minimum and critical maximum as the iguanid *Dipsosaurus dorsalis*. *Chamaeleo namaquensis* cannot be described as thermophilic, but it is active over a narrower span of body temperatures (25.7 C) than *C. pumilus*. There are no other data on chamaeleon body temperatures in the field, so the thermal situation of *Chamaeleo pumilus* and *namaquensis* with other chamaeleonids cannot be discussed reasonably.

5. Thermoregulation: warming/cooling in the field

Chamaeleo pumilus and *C. namaquensis* thermoregulation is a complexly integrated process, involving dermal colour lability with attendant vasomotor and other cardiovascular adjustments, body posturing, thermo-pneumatic changes in lung and air sac volume, and panting.

Table 7 gives the skin colour and body compression indices referred to in this study. Body compression 'I' was the initial warming posture used by *C. namaquensis* and *C. pumilus* earliest and latest in the day, and occasionally during cool or unfavourable days to maintain body temperatures close to preferendum. It is also the resting position, being modified to initial warming by the chamaeleon assuming colour index '5' and positioning so that both sides of the body were usually in the sun, allowing the slanted rays of the rising or setting sun to strike the chamaeleon's body as directly as possible. Such a position gives the body a spherical shape and aids the warming of the upper part of the body, the lungs, air sacs, and probably the dorsal aorta. At this time the air sacs in *C. namaquensis* are inflated (Fig. 12B). In *C. namaquensis* this posture was coupled with thigmothermic behaviour. On chilly, foggy winter mornings coastal *C. namaquensis* experienced environmental temperatures of 8 C. The chamaeleons assumed body compression 'I' and colour index '5' and were closely adpressed to, but not ploughed into the substrate. The tail and legs were held close to the body. Such behaviour minimizes convective heat loss and thermoregulatory ploughing has no value, since temperatures warmer than that at the surface do not occur until a depth of 150 mm and greater. Under these weather conditions, the body temperatures and skin surface temperatures of the chamaeleons were no lower than 14.0 C. The substrate surface temperature directly beneath the animal is warmer by one or two degrees to that of exposed substrates. The animals remain still, moving out only for passing prey, territorial challenges, and courtship.

Under fair skies *C. namaquensis* ploughed thermoregulatory warming grooves in the substrate. In the mornings, such grooves were dug no deeper than 5 mm, but in late afternoons and evenings such grooves were ploughed to a depth of 15 mm. Digging deeper grooves later in the day allowed *C. namaquensis* to experience substrate temperatures a few degrees higher than that at the surface, whereas early in the day temperatures higher than that at the surface are only realized at depths of 150 mm and greater. However, a shallow groove early in the day minimizes convective heat loss, especially in the strong

Table 7
Colour and body compression indices for *Chamaeleo pumilus* and *C. namaquensis* in the field and in the laboratory studies.

Body Compression Index				
Both species	I	II	III	IV
	body oval in cross section and adpressed to substrate with legs held to body	body cylindrical in cross section legs held away from and raising body from substrate	legs and body essentially as in 'II' but body slightly laterally compressed, especially dorsad; body width reduced 10% from that of 'II'	legs in stiff-legged stance directly under body; body an exaggeration of 'III'; extreme lateral compression; body width reduced by 30% from that of 'II'
Colour Index*				
<i>C. pumilus</i> **	0	1	2	3
	pallor	yellow	pale green	medium green
<i>C. namaquensis</i>	4	5		
	dark pink, light gray, or sulphur yellow	ground colours dark pink, light gray, sulphur yellow, or light green; blotched or spotted pattern may occur	dark gray or maroon, or dark, vitreous brick red ground colour, with dis-tinct pattern	dark purple to black; usually uniform, pattern of white lateral spots indistinct if rarely present

* As that of Hogben (1924) (See also Zood & Eyre 1934).

** Valid only for adults and juveniles with adult pattern. Other juveniles are either slate gray, light or dark brown, or black, thus are only '0' and '5', possibly '1'.

winds occurring under fair skies, and the slightly deeper grooves later in the day have the same value with the added benefit of a heat source. *C. namaquensis* periodically ploughed along uncovering more warmth as that at one site dissipated. *C. namaquensis* occasionally selected sheltered sites to the lee of dead vegetation, rocks, and other objects. The efficiency of initial heating within one hour is given in Table 8. *C. namaquensis* body temperatures increased by 9.5 C in the first 20 minutes after which heat uptake slows. Heating during the warmer season was somewhat faster, but the environmental temperatures were also higher.

Table 8

Efficiency of initial warming over the sixty minute period after sunrise (cool season only), in *Chamaeleo pumilus* (Cp) and *C. namaquensis* (Cn). Body compression ('CmI') and colour index ('CII') are given in Table 7.

Temperatures (°C) increase		N			
Environmental	Body	Species	CII	CmI	Weather
8,0-10,0	14,0-25,0	6 Cn	5/5	I	fog, no wind
13,0-13,8	18,0-29,0	8 Cn	5/5	I	clear, strong wind
5,0-10,8	6,0-25,0	14 Cp	5/5	I	clear, light to moderate wind
13,0-14,5	12,0-20,0	10 Cp	5/5	I	rain, strong wind

Chamaeleo pumilus followed much the same mode as to body compression and colour indices as described above for *C. namaquensis*, except for use of substrates. Occasionally, *C. pumilus* would use metal objects (e.g. iron railings) acquiring some thigmothermic value as those selecting somewhat wind-protected sites. *C. pumilus* lacks air sacs, but the lungs are long, the distal parts of which might serve the same function as the air sacs in *C. namaquensis*. During warming and cooling thermoregulation, the lungs of *C. pumilus* and air sacs of *C. namaquensis* were brought to maximum volume, as can be deduced by the inflated appearance of the body in the field, palpating, and verified surgically. The efficiency of *C. pumilus* when warming is given in Table 8. As in *C. namaquensis*, the fastest heat increase was in the earlier basking period, when *C. pumilus* body temperatures increased by 14 C in the first 15 minutes, the environmental temperature increasing only by one degree in the same period. Warmer season body temperature heating rates were as in *C. namaquensis*.

When initial warming has taken place, both chamaeleons switched to body compression 'IV'. In body compression 'IV' the body is greatly laterally compressed, reducing body width to 30% of normal, and the skin between the scales is greatly stretched. Usually only one side at colour index '4-5' was presented to the sun, the side in the shade being considerably lighter, usually at colour index '2'. Warming *C. namaquensis* at colour index '5' and body compression 'IV' with the skin thus stretched, have some of the scales edged in, and small flecks of the skin yellow and red. The whole body was positioned to receive the rays of the sun as directly as possible. The temperature of the side in the sun was read with a shielded probe and was at or slightly above that

of the body; the side in the shade at, or a few degrees below. The chamaeleons periodically changed position, so that the side presented to the sun became the side in the shade and vice versa. The hue of each side changing during the turn around, so that the side facing the sun was always a darker colour, such as '4' or '5', and the side in the shade always lighter. They performed thus, even if the weather was overcast, presenting to the obscured sun.

Postural changes and assumption of different hues during the day varies somewhat with the environmental conditions, such as temperature, wind, cloud cover and rain. It must be noted here that chamaeleons in apparently identical situations were not necessarily the same colour, though body temperatures were about the same. Close observation revealed that the light phase ones assumed darker hues as their body temperatures dropped below the thermal preferential, and as their body temperatures rose their hues again lightened. In short, dark chamaeleons are raising their body temperatures to preferential. Chamaeleons at a colour index of '2-3' are at preferential. Fine adjustments included varying the side exposed to the sun. Efficiency of temperature maintenance is given in Table 9.

Table 17, showing thermoregulation through the seasons, veils important aspects by giving these data inclusively. For example, it amply shows the range of environmental and body temperatures per season for different weather conditions, but also implies that the higher body temperatures occurred with the higher environmental temperatures. This is not so, as most high body temperatures were recorded with lower environmental temperatures. This is brought out in Table 9, but *C. pumilus*, for example, 'Cool Fair', June 5, 11:00 hours, moderate south-west wind, environmental temperature (50 mm) 14.5 C; body temperatures ($N = 5$) 20.9-23.6 C ($\bar{x} = 22.5$ C). This is also true of *C. namaquensis*; 'Cool Fair', April 14, 12N, calm, substrate temperature 55.5 C; body temperatures ($N = 5$) 30.0-36.2 C ($\bar{x} = 33.1$ C).

Thermoneutrality occurs when the chamaeleon does not have to regulate to maintain thermal preferenda. This condition is realized with environmental temperatures of 23.0-26.0 C for *Chamaeleo pumilus* and 26.0-32.0 C for *C. namaquensis* under calm conditions. At such time they assumed a body compression of 'II', sometimes 'III', and skin colour of '3', and in some instances '2', which are the upper levels of the thermoneutrality zone. Dermal temperatures of both sides were about the same and close to the body temperatures. In *C. namaquensis* the air sacs were not in use, and in *C. pumilus* the lungs not filled to full volume. Also, the tail and legs were not held closely to the body.

As environmental temperatures soared, chamaeleons responded by reversion to body compression 'IV', rarely 'III', but never 'I' or 'II'. Colour was always '2' or lower, and the side to the sun lighter than the side in the shade. Complete pallor was assumed with a body temperature of 39.0 C for *C. pumilus*, and 30.0 C for *C. namaquensis* at abnormally high environmental temperatures. The lungs and air sacs filled and expelled air rapidly, and panting ensued. *C. namaquensis* was interesting in that occasional irregular panting with the

Table 9

Efficiency of body temperature maintenance in *Chamaeleo pumilus* (Cp) and *C. namaquensis* (Cn) selected to show extremes over the sixty minute midday period. See Table 7 for compression and colour indices.

Temperatures (°C)		Body		Colour index		Body		Weather		Season	
Environmental	Range	\bar{x}	Range	\bar{x}	Species	Sun	Shade	compression index	Weather	Season	
14,7-15,0	(14,8)	20,0-25,0	(23,0)	5	10 Cn	5	5	IV	fog/drizzle, light to moderate wind	C	
18,2-28,0	(23,1)	27,5-33,0	(30,0)	2-3	11 Cn	2-3	2-3	IV	clear, strong wind	O	
16,0-16,5	(16,3)	20,0-23,5	(22,8)	5	19 Cp	5	5	I	rain, moderate to strong wind	O	
17,0-20,8	(18,9)	22,8-30,8	(26,8)	2	14 Cp	2	2	IV	clear, strong wind	L	
20,4-39,8	(30,1)	29,0-31,5	(30,3)	3-5	23 Cn	3-5	3-5	I	fog/drizzle, light to moderate wind	W	
45,0-67,0	(56,0)	33,6-34,2	(33,9)	0-2	18 Cn	0-2	0-2	IV	clear, strong wind	A	
26,6-39,0	(34,3)	30,0-35,0	(32,5)	1-2	15 Cp	1-2	1-2	I	clear, strong wind	R	
20,0-27,0	(22,7)	26,0-34,8	(30,4)	3-5	15 Cp	3-5	3-5	I or IV	rain, moderate to strong wind	M	

mouth barely open starts at a body temperature of 27.0–32.0 C, becomes periodic and regular at a body temperature of 36.0–37.0 C and continuous at a body temperature of 39.0 C, when the mouth is more widely open and the tongue gorged with blood and raised from the floor of the mouth. There was no preliminary panting in *C. pumilus*; juveniles began continuous panting with a body temperature of 33.1 C and adults at 37.0 C, with the mouth widely agape, the labial scales bulged outward, and the tongue much engorged with blood above the floor of the mouth.

Towards the end of the day, as solar insolation wanes and environmental temperatures drop, chamaeleons resort to darker hues ('4–5') and body compression 'I' and thigmothermic behaviour—including ploughing in *C. namaquensis*, and body compression 'IV' in *C. pumilus*. In short, the whole thermoregulatory process towards the end of the day is essentially a repeat of early morning warming. The loss of body temperatures over a period of one hour is given in Table 10.

Table 10

Fall of environmental and body temperatures of *Chamaeleo pumilus* (Cp) and *C. namaquensis* (Cn) over the one hour prior to sunset during the cool season.

N species	Temperatures (°C) loss		Weather
	Environmental	Body	
15 Cn	20.0–18.0	29.5–29.0	fog, light/variable wind to calm
19 Cn	35.0–24.0	29.0–27.0	clear, strong wind
17 Cp	16.0–13.0	23.0–21.0	rain, moderate wind
40 Cp	21.5–13.0	28.0–25.0	clear, light/variable wind

N.B.—Compression and colour indices for this time span are essentially as in Table 8.

6. Thermoregulation

Warming/cooling in the laboratory: Under artificial and natural conditions live chamaeleons heated faster than they cooled, while dead ones heated and cooled at the same rate. Table 11 shows *Chamaeleo namaquensis* and *C. pumilus* over a period of 300 minutes in total darkness and Table 12 in light. Equivalent results were obtained for a similar test with light and darkness alternated. It is apparent that skin colour liability does enable chamaeleons to raise and lower their body temperatures (Table 11). In the dark, no skin hue above colour index '2' was recorded. The rise of body temperatures was slow and it should be noted that both animals, though previously held at –5.0 C before the run, maintained body temperatures above –5.0 C. *C. namaquensis* body temperatures ranged from –2.0 to 1.9 C (\bar{x} = 0.7 C); *C. pumilus* body temperatures ranged from –3.0 to –1.0 C (\bar{x} = –2.5 C). Skin surface temperatures were equivalent in both animals throughout the experimental range. Body temperatures, especially those of *C. pumilus*, are considerably below the higher experimental temperatures.

Table 11

Body compression ('CmI' in roman numerals), colour changes ('CII' in arabic numerals), and body temperatures of 10 *Chamaeleo pumilus* and 10 *C. namaquensis* in total darkness at various experimental temperatures (all temperatures degrees Celsius). See Table 7 for compression and colour indices.

Time from o in mins	Exptl temp.	<i>Chamaeleo namaquensis</i>				<i>Chamaeleo pumilus</i>							
		CmI	CII	Skin temperature Range	Mean	Body temperature Range	Mean	CmI	CII	Skin temperature Range	Mean	Body temperature Range	Mean
30	-5.0	I	0	-4.0 to -5.0	-4.6	-2.0 to 1.9	-0.1	I	0	-4.0 to -5.0	-4.6	-3.0 to -1.0	-2.5
60	5.4	I	2	3.1 to 3.9	3.6	2.4 to 2.7	2.5	I	0	3.5 to 4.0	3.7	3.5 to 4.7	4.5
90	8.6	I	1	6.0 to 7.5	6.8	5.5 to 6.8	5.9	I	2	7.0 to 8.5	7.6	7.0 to 8.0	7.3
120	11.9	I	2	10.3 to 10.9	10.6	9.4 to 12.0	11.1	I	1	10.3 to 10.8	10.6	10.6 to 12.0	11.2
150	13.8	I	2	13.2 to 14.0	13.8	13.1 to 14.1	13.6	I	1	13.6 to 14.2	13.8	13.0 to 14.1	13.4
180	14.6	IV	1	15.3 to 16.3	16.0	17.0	17.0	III	2	15.0 to 15.9	15.5	16.1 to 16.6	16.3
210	20.3	I	2	20.0 to 20.9	20.6	21.9 to 24.0	23.5	I	1	20.0 to 20.5	20.3	21.0 to 22.9	22.1
240	23.0	II	2	21.6 to 23.5	22.1	20.3 to 23.7	22.1	II	2	21.6 to 23.5	22.1	21.5 to 23.5	22.1
270	30.1	III	2	26.7 to 30.0	27.5	26.9 to 29.1	27.5	III	1	28.0 to 28.6	28.3	27.1 to 29.0	28.4
300	40.0	IV	1	28.0 to 29.9	28.6	29.9 to 31.1	30.0	III	2	26.5 to 29.9	27.4	28.8 to 30.8	29.4

Table 12 shows the results with these animals exposed to light. Active thermoregulation in *C. namaquensis* did not occur until the experimental temperature reached 5,0 C and was markedly so at 15,0 C; two degrees above voluntary torpor for this species. However, *C. pumilus* actively thermoregulated at the lowest experimental temperature. Dark phase (colour index '4-5') was evident on the light facing side of the animals at experimental temperatures, -4,5 to 25,0 C (*C. pumilus*) and 5,9 to 25,0 C (*C. namaquensis*). Thermoneutrality occurred in both species at experimental temperature 30,0 C, and cooling with light hues and less of body side presented to the light at experimental temperatures of 35,0 C and above. Body compression and panting were as in field observations.

Table 12

Body compression ('CmI' in roman numerals), colour changes ('CII' in arabic numerals), and body temperatures of 10 *Chamaeleo pumilus* and 10 *C. namaquensis* in the light at various experimental temperatures. See Table 7 for compression and colour indices. Below, 'T' denotes time from 0 in minutes.

<i>Chamaeleo namaquensis</i>										
T	(°C)	CmI	Skin temperatures (°C)						Body temperatures (°C)	
	Exptl temp.		Side to the light			Side to the dark			Range	Mean
			CII	Range	Mean	CII	Range	Mean		
30	-4,5	I	3	3,1- 3,3	3,3	1	1,2- 1,3	1,3	1,0- 1,9	1,7
60	2,5	I	3	4,8- 5,5	5,1	1	3,0	3,0	3,0- 4,4	3,9
90	5,8	I	4	7,8-10,0	9,1	2	6,9- 8,4	7,8	6,8- 8,5	8,1
120	15,0	IV	5	14,3-25,5	18,2	1	11,3-16,2	13,3	12,4-22,9	16,3
150	17,0	III	5	16,4-26,0	23,7	1	15,2-17,9	16,6	16,5-25,0	21,7
180	18,0	IV	5	21,1-27,6	26,2	1	19,0-20,5	20,2	20,3-26,9	24,9
210	25,0	III	4	27,5-33,5	31,6	2	24,0-25,0	24,6	27,5-32,0	30,8
240	30,0	III	2	28,4-33,3	31,3	1	26,5-31,0	27,7	26,2-32,6	29,4
270	35,0	IV	1	30,3-37,0	32,0	2	29,7-35,8	30,7	30,8-37,6	32,6
300	42,0	IV	0	35,0-36,0	35,6	2	33,0-34,9	34,3	34,7-35,7	35,2

<i>Chamaeleo pumilus</i>										
T	(°C)	CmI	Skin temperatures (°C)						Body temperatures (°C)	
	Exptl temp.		Side to the light			Side to the dark			Range	Mean
			CII	Range	Mean	CII	Range	Mean		
30	-4,5	I	5	1,1- 1,2	1,2	2	-0,5- 0,0	-0,5	0,4- 0,6	0,6
60	2,5	I	5	3,5- 5,5	4,9	2	2,5- 4,0	3,3	3,5- 5,0	4,3
90	5,8	III	5	8,0- 9,0	8,5	2	6,3- 7,5	7,2	7,0- 9,0	8,5
120	15,0	IV	5	13,5-22,7	17,5	3	12,3-17,0	13,3	13,8-20,0	17,2
150	17,0	IV	4	15,1-23,5	22,0	2	14,5-17,0	16,0	17,0-22,0	20,5
180	18,0	IV	4	19,0-27,0	25,5	2	17,0-19,3	18,3	19,9-25,0	23,5
210	25,0	IV	4	27,6-29,5	28,2	2	23,0-24,0	27,0	27,0-28,0	27,4
240	30,0	IV	3	27,1-33,5	28,8	2	25,9-30,9	32,3	25,9-32,8	27,8
270	35,0	IV	1	31,2-34,8	32,3	1	31,0-33,2	31,7	31,0-35,0	32,3
300	42,0	IV	0	32,7-34,9	33,5	2	32,7-34,9	33,5	34,2-35,0	34,3

Table 13 shows thermoregulation of chamaeleons in an outdoor enclosure. These results were similar to those of field temperatures and need no further discussion.

Table 13

Effect of rising experimental temperatures in an outdoor enclosure on the thermoregulation of 10 *Chamaeleo namaquensis* and 10 *C. pumilus*, showing body compression ('CmI' in roman numerals), colour changes ('CII' in arabic numerals), skin, and body temperatures. Air temperature at five centimetres (T_a 50 mm) is the experimental temperature for *C. pumilus*; and temperature of red Namib dune sand (T_s) is the experimental temperature for *C. namaquensis*.

Below, 'T' denotes time in minutes. See Table 7 for compression and colour indices.

<i>Chamaeleo namaquensis</i>										
(°C) Exptl temp.		Skin temperatures (°C)							Body temperatures	
		Side to the light				Side to the dark			(°C)	
T	T _s	CmI	CII	Range	Mean	CII	Range	Mean	Range	Mean
0	8,8	I	5	8,0-9,5	8,8	1	9,3-11,0	10,0	8,5-10,5	9,6
30	16,5	IV	5	19,0-21,0	20,3	1	14,5-16,3	15,3	17,0-19,5	18,5
60	32,0	II	2	33,5-36,4	35,5	1	31,7-33,6	32,7	32,0-34,0	33,3
90	39,0	IV	1	32,5-36,0	34,5	2	33,0-35,5	34,0	36,0-39,5	38,6
120	50,0	IV	1	30,7-33,1	31,7	2	30,5-32,5	31,8	35,0-38,6	36,7
150	55,0	IV	0	24,5-28,0	25,7	1	23,5-27,0	25,3	33,5-38,0	35,7

<i>Chamaeleo pumilus</i>										
(°C) Exptl temp.		Skin temperatures (°C)							Body temperatures	
		Side to the light				Side to the dark			(°C)	
T	T _a 50 mm	CmI	CII	Range	Mean	CII	Range	Mean	Range	Mean
0	8,8	IV	5	7,7-9,1	8,5	2	8,0-9,5	8,5	8,5-10,3	9,3
30	15,0	IV	5	8,9-11,0	10,0	1	8,8-10,5	9,5	10,8-12,7	12,0
60	30,0	IV	3	18,5-20,5	19,7	2	18,0-19,5	19,0	23,5-26,0	25,3
90	35,0	IV	1	23,5-26,5	24,5	1	23,0-25,0	24,1	35,0-38,3	37,5
120	35,0	IV	1	22,0-24,9	22,7	2	21,5-23,5	22,5	32,0-36,0	34,3
150	37,0	IV	1	23,3-26,0	24,3	1	22,9-25,5	23,8	31,0-35,0	33,3

Comparing thermoregulation data collected in the field and laboratory it appears that the results are similar. But the slight discrepancy that occurs between field and laboratory are assignable to the fact that the animals in the laboratory tests were strapped so that they could not readily alternate body sides in presentation to the heat source, as demonstrated by the results of those in the outdoor enclosure which could alternate body sides and agree with the field data. This 'minor' variance seems important to the chamaeleons for fine thermoregulation. It must be noted that some chamaeleons never accepted being strapped down or in other ways adapting peaceably to the experimental process, regardless of the acclimation period.

7. Cardiac rate and temperature

The heart rate of *Chamaeleo pumilus* and *C. namaquensis* during heating and cooling was greater during rising body temperatures and lower during falling body temperatures at the same experimental temperature (Table 14). The values are similar to that Bartholomew *et al.* (1965) give for the scincid *Tiliqua scincoides*, and Bartholomew & Lasiewski (1965) give for the iguanid *Amblyrhynchus cristatus*. The elevation in chamaeleon heart rates at higher temperatures

is assignable to the panic and frantic activity shown by both species at these levels. *C. pumilus* and *C. namaquensis* during cooling slightly elevated heart rates when their respective thermal preferenda were reacquired during cooling, as apparently does *Amblyrhynchus*. Again it must be noted that the cardiac rate of chamaeleons must be high, since no specimen adjusted to the test, nor was quiet during readings, their violent struggles being reflected. They seemed particularly irritated by the probe, which they made frantic efforts to dislodge. Therefore, except for the lower temperatures from 5 to 10 C, when *C. namaquensis* is torpid, the readings given are for very active animals.

Table 14

Heart rates of 5 *Chamaeleo pumilus* and 5 *C. namaquensis* in relation to heating and cooling at various temperatures.

Temp. °C	<i>C. namaquensis</i>		<i>C. pumilus</i>	
	Cooling	Heating	Cooling	Heating
5	2,0	0,9	5,0	20,0
10	3,0	6,0	18,0	45,0
15	10,0	44,0	31,5	85,0
20	30,0	110,0	85,0	190,0
25	38,5	150,0	100,0	215,0
30	40,0	160,0	95,0	205,0
35	50,0	151,3	100,0	185,0
40	65,0	100,0	125,0	200,0
45	77,0	105,0	no record	

8. Summation of chamaeleon thermoregulation in comparison with other reptiles; role of colour

In summarizing and comparing chamaeleon thermoregulation with other reptiles, it should be noted that the known saurian usage of physiological temperature control methods are: (1) toleration of hyperthermia, which is non-existent in *Chamaeleo namaquensis* (maximum voluntary body temperature, 39,7 C), or *C. pumilus* (maximum voluntary body temperature, 37,0 C); (2) changes in surface-volume ratio by body contraction and expansion; (3) changes in reflectivity; (4) changes in the cardio-vascular system affecting heat transport through the tissues.

The ability of chamaeleons to change colour is the most noticeable integral part of chamaeleon thermoregulation. Aristotle (Crosswell's translation 1883) and Pliny (Bostock & Riley's translation 1887) first recorded that chamaeleons change colour, the former suspecting this to be a response to light and temperature. But it is an old fallacy that they do so to match their background, and such background-matching as does occur is the exception, not the rule, and quite incidental to the thermoregulatory function. It seems absurd that background-matching is so widely held—yet so easily disproved by direct observation. No studies have measured actual body and dermal temperatures at the varied hues, and their relationships to environmental temperatures or conditions.

This study has reported environmental temperatures and conditions, body

temperatures and dermal temperatures at different hues in an integrated manner in the field and laboratory and in concert with other chamaeleonid thermoregulatory processes. From this it is concluded that colour change in *Chamaeleo pumilus* and *C. namaquensis* is primarily thermoregulatory, secondarily camouflage, and least important is background-matching.

Colour lability is a widely recorded phenomenon in invertebrates. The teleost fishes are the most proficient of colour labile vertebrates. For example, plaice can even match checkerboards and mosaics. Many reptiles, mostly the small desert saurians, have a wide range of colour change, and the agamid genus *Calotes* has probably the most versatile colour repertory. The young of some larger forms are colour labile, such as *Sauromalus obesus*, *Alligator mississippiensis*, and *Crocodylus niloticus*. There are pattern component changes in *Iguana iguana*. The tortoise *Chelodina longicollis* (Woolley 1956) is colour labile. The largest living lizards (Varanidae) are not colour labile, perhaps because they enjoy true endothermy by virtue of their size and proven physiological ability (Bartholomew & Tucker 1964). Rahn (1940, 1941) and Norris (1967) also discuss colour change in snakes of the genus *Crotalus* (Crotalidae), the deserticolous *Crotalus cerastes* being the most versatile at colour change.

The mechanics of chamaeleon colour change are mediated by expansion and contraction of melanophores in the first, innermost layer of the thick dermis. In expansion, the melanin extends into tentacle-like arms towards the surface through the other three dermal layers, which are: a uniform layer of white-reflecting cells; an irregularly distributed layer of blue-reflecting cells; an outer dermal layer composed mostly of xanthophores and a few erythrophores. The thin, transparent epidermis covers these dermal layers. The white-reflecting and blue-reflecting cells contain no pigment but intracellular-layered crystalline structures of guanine.

The blue- and white-reflecting cells do not function in colour change, but the xanthophores and erythrophores contract and expand, acting as a screen to give weaker or stronger effects. The blue-reflecting cells under the xanthophores give the typical green hue in a chamaeleon. The main effectors of chamaeleon colour change, the melanophores, disperse melanin into the cell arms which penetrate the other layers to mask one or more of them. Light green or yellow is mediated by melanin contracted below the white-reflecting layer, and the dispersal of melanin masking white reflection results in dark green. If melanin is dispersed over the xanthophores, the chamaeleon appears black.

Reptiles with the ability to change colour have the same complement of chromatophores as that described for chamaeleons, or some items missing, but all have melanophores, the chromatophores necessary for colour change.

Questions about colour change revolve largely around control of the colour mediating structures and secondarily the value to the animal of such change. It is not the purpose of this study to undertake detailed examination of the former, but an understanding of the latter is important as to how chamaeleons use colour change to maintain themselves in dynamic equilibrium

with their environment.

Detailed studies on reptilian colour response, with valuable literature reviews in some, should be consulted in Atsatt (1939), Brücke (1852), Fuchs (1914), Hogben (1924), Hogben & Mirvish (1928a, b), Kleinholz (1938a, b, 1941), Krüger & Kern (1924), Longstaff & Poulton (1907), May (1924), Parker (1932, 1938, 1948), Rahn (1940, 1941), Redfield (1918), Sand (1935), Walls (1942), Weber (1881), Zoond & Bokenham (1935), Zoond & Eyre (1934), for early work, and Canella (1963), Coleman & Livezey (1968), Fingerman (1965), Hoesch (1961), Norris (1967), Talbot & Livezey (1964) and Waring (1963) for recent studies. Cleworth (unpublished data) is examining the electrophysiology of chamaeleon colour change by studies involving electron microscopy, skin reflectivity at dark and light adapted states, and light magnitude necessary to evoke change. Fingerman's (1965) and Waring's (1963) reviews provide excellent treatment of colour changes in all animals; the latter dealing only with vertebrates.

Colour change in reptiles is under nervous control in the chamaeleonids (Brücke 1852; Hogben & Mirvish 1928a, b; Zoond & Eyre 1934; Zoond & Bokenham 1935; Farghaly 1941), endocrine only in the iguanid *Anolis* (Kleinholz 1938a, b; May 1924), and dual in the iguanid *Phrynosoma* (Redfield 1918; Parker 1928). Part of the confusion of what mediates control is simply answered by different animals using different methods, as such would be expected in a polyphyletic group.

Canella (1963) questioned Hogben & Mirvish's (1928a, b) findings on chamaeleonids that epinephrine is not involved in excitement pallor, an error suggested by Parker (1938). Canella also found MSH, intermedin, ACTH, acetylcholine, pilocarpine, and atropine cause darkening. However, the presence of pigment concentrating nerves of the autonomic system in chamaeleons is still widely accepted. Perhaps complicating the picture still further is that all workers on chamaeleonids used species from different species groups (Farghaly: *Chamaeleo vulgaris* = *C. chamaeleon*; Canella: *C. jacksoni*; Zoond and co-workers: *Lophosaura pumila*; Hogben and Mirvish: *C. pumilus*, the latter two now synonymous with *C. pumilus*). The confusion of the identity of the last workers' subjects is reflected in Waring's (1963) review.

Cleworth (unpubl. data) has kindly summarized for me the results of his study on *Chamaeleo dilepis*, *C. zeylanica* (= *C. chamaeleon*), *C. pumilus* and *C. jacksoni*. Work on the last two species was discontinued, because the rough texture of their skin made reflection analyses difficult. Cleworth standardized ambient temperatures (22.0–25.0 °C) to investigate effect of light on light- and dark-adapted animals. He found the skin of chamaeleons shows marked spectral sensitivity. Cleworth found that dark-adapted chamaeleons absorb heat, which is of considerable value at low temperatures. *C. pumilus* darkens to a greater degree than other chamaeleons. Heating effect of light-adapted chamaeleons is negligible, and is of reflective value at high temperatures. Regional differences in skin texture are not demonstrable, that is, the sides, the

back and the belly are equally reflective. *C. pumilus* is not quite as reflective as *C. dilepis* (*C. namaquensis* would be more similar to *C. dilepis*), though this may not be owing to texture. Chamaeleons absorb a large percentage of incident light, especially at the near infra-red, with two main absorption peaks corresponding to those for water. More light passes through individuals with stretched skin, and all 'extra' transmission is through the inter-scale skin. Melanin acts as a 'flat black' substance over the whole spectral range (300–2 700 m μ). Cleworth observed migration of the allophore granules. Subcutaneous injection of MSH caused the injected area to go very black, giving an idea of maximal response. An area of illuminated skin can act independently, and response of the system to light is rapid, especially darkening.

Complicating studies of colour lability in *Chamaeleo namaquensis* are geographic variance of ground and colour pattern, which are discussed in the reproduction section. Hoesch (1961) gives an interesting account of the colours and patterns of this species. He found *C. namaquensis* is whitish gray at environmental temperatures up to 37,0 C, and that it becomes pallid at an environmental temperature of 40,0 C. Hoesch feels this is an adaptation to the desert in which it lives. He mentions the variation of black coloration covered with equidistant small white spots, and the variety of colour with pattern, which make assignment of colour indices a problem in this species. Hoesch also records a 'Schreckmuster' (fright muster) *C. namaquensis* assumes when confronted by a predator, for example a snake, *Bitis caudalis*. It is doubted that it is a fright muster, since *C. namaquensis* assumes it when suddenly sighting a food item (Fig. 8), or a mate (usually only females). Furthermore, an angry chamaeleon (see defence in section on behaviour, p. 73) assumes uniform black (colour index '5'). Thus, it is felt that colour index '5' is the fright or intimidation hue of angry *C. namaquensis*, as with *C. pumilus*, and this seems true of most chamaeleonids. Until further data are forthcoming, Hoesch's 'fright muster' is best considered an 'excitement pattern'. The speed of change (<1,6 secs) from uniform pallor completely to this excitement pattern and/or colour index '5' seems to indicate neutral control.

That chamaeleonid melanophores are served by pigment concentrating nerves of the autonomic system is generally accepted. The problem is do the nerves themselves mediate dispersal and contraction, is it humoral, or neuro-humoral? Zoond & Eyre (1934) found nerve transection caused darkening of that part of the skin served by the severed nerve. Parker (1938) suggested that darkening of the skin area after nerve transection is due to excessive stimulation by 'injury currents', whereas Sand (1935) thought it due to lack of stimulation. That is, no nerve to carry the message equals no response, or darkening. It was frequently observed in wild and captive *Chamaeleo pumilus* and *C. namaquensis* that injuries inflicted in territorial conflicts were a perfect pallid outline of the attacker's teeth when the injured chamaeleon was dark (colour indices '4–5'), but the injuries were colour indices '4–5' when these same chamaeleons were lighter (colour indices '<2'). A large *C. namaquensis*

attempting to eat a *Bitis peringueyi* was observed in the field. The viper bit the chamaeleon on the dorsum in the pelvic region. The fang punctures went black, surrounded by a small, pallid area. Within a week, these injury reactions normalized. Of further interest, an ailing *C. namaquensis* was injected intramuscularly in the tail, with 125 000 units of procaine penicillin and 0.12 g dihydrostreptomycin ('Strypen', May & Baker Co.). Ten minutes after the injection the left side of the head was black and the right side of the head was pallid, but the rest of the body was all black. Fifty minutes after the injection this chamaeleon was uniformly black. This might indicate that the antibiotic interfered with colour lability on an intracellular or enzymatic level.

Somewhat more drastic to the chamaeleons was the observation that before decapitation, all chamaeleons were uniformly black with rage, but upon beheading the body became instantly pallid while the severed head remained black. This reaction did not occur unless the spinal cord was cut, and would indicate CNS colour control of a high order of integration.

Ailing chamaeleons cannot readily change colour. The symptoms and some etiological agents are given in the section on parasitism and disease in mortality (see p. 31). Such affected chamaeleons were always pallid, and unable to effectively thermoregulate (Table 15). They were unable to warm as fast as normal chamaeleons who could assume colour index '5'. Diseased chamaeleons also cooled at a faster rate. At higher ambient temperatures the thermal relationships of sick and normal *C. namaquensis* seemed to be the same. Although some thermoregulatory aids still functioned, it was apparent that even they were less effective with an upset in thermo-colour-lability, and its attendant postural changes. Diseased chamaeleons were rarely other than body compression index '1'. The skin temperature of such afflicted chamaeleons was that of the ambient air temperature. Also *C. namaquensis* with pneumonia seemed quite unable to warm or maintain heat. Unfortunately, all these data are for captives, though individuals in the wild would be more vulnerable to weather conditions and certainly to predation. Diseased chamaeleons eat sparingly, if at all, and their high metabolic rate dwindles. This indicates that colour lability is important in thermo-homeostasis of *C. namaquensis* and comparable data for *C. pumilus* are available.

Table 15

Thermoregulatory efficiency of diseased and healthy *Chamaeleo namaquensis*.
Temperatures are in degrees Celsius. Means are shown in parentheses.

Time from o in mins	Exptl T _s	temps T _a 50 mm	Healthy (N = 7) Body temperatures Range	Diseased (N = 6) Body temperatures Range
30	10.0	10.0	9.5-12.0 (10.5)	7.5-9.5 (8.5)
60	17.0	15.0	18.5-21.0 (20.0)	13.0-14.5 (13.7)
90	33.0	30.0	33.5-35.5 (34.3)	27.0-29.0 (28.0)
120	50.0	35.0	36.5-39.0 (37.5)	34.0-37.5 (36.0)
150	55.0	35.5	36.5-39.0 (37.5)	36.5-39.0 (37.5)
180	45.0	25.0	36.5-39.0 (37.5)	26.5-28.5 (27.5)

Longstaff & Poulton (1907) discuss the only protective value that colour may have for *C. pumilus*. Warming in the morning, a chamaeleon laterally compressed at body compression index 'IV' is black at colour index '5' on the side to the sun and light at colour index '2' on the opposite side, with the venter rather static at colour index '2'. This counterbalances the diminution of natural illumination from the open sky as the eye scans from the back to the sides to the venter on the animal, thus neutralizing shadow and conspicuousness. The light hue of the shade side neutralizes shadow, and the highly illuminated side presented to the light source is toned down by being dark, so the overall effect is to dissipate solidity. The ornamental knobs and crests disrupt the body outline melting the chamaeleon into its background. Such protective coloration may be most valuable to a chamaeleon warming during the cooler times of day, when assumption of dark (colour index '5') to the sun also has thermoregulatory value in absorbing warmth. Weber (1881) first proposed that dark coloration serves chamaeleons for warmth absorption and light for cooling. At hotter times of the day, assumption of a lighter hue facing the sun for cooling had less camouflage value depending where the *C. pumilus* was and it frequently selected sites which it did not match. The best overall matching were for chamaeleons on reeds surrounding vleis. The nocturnal resting hue (pallor) of *C. pumilus* made it quite conspicuous, and may be due to the old response of melanophores to contract in the dark.

It is generally regarded that chamaeleons cannot turn or acquire reddish hues, though erythrophores are in the dermis. On the reddish, interior Namib Desert dunes, most inhabitant *Chamaeleo namaquensis* have a pinkish or reddish ground colour with a pattern of brick-red blotches. On the grayish-white coastal dunes, most inhabitant *C. namaquensis* have a basic ground colour of sulphur yellow with a pattern of brownish or reddish blotches. But when warming, both inland and coastal phases of *C. namaquensis* assumed black (colour index '5') and on their respective substrates alone they were most conspicuous, especially on foggy mornings. However, where there were scattered debris on their highly contrasting substrates, the chamaeleons at colour index '5' appeared as artifacts and not readily noticeable. The colour variants of *C. namaquensis* are most difficult to see at colour indices of '<2' on their respective substrates.

Thus, reds, especially dark reds, may have the same thermoregulatory benefits of other dark colours, but a dark red chamaeleon in a green bush on a cold day would be noticeable and more vulnerable to predation. But a dark green chamaeleon on red or whitish-gray desert sand would also be conspicuous. Thus it is felt that red is beneficial for the Namib Desert dune-dwelling *Chamaeleo namaquensis*, just as a sulphur yellow or yellowish ground colour is concealing and valuable in thermoregulation for coastal Namib dune dwellers. Towards the better-watered and vegetated Great Western Escarpment at the eastern edge of the Namib, very dark greens appear in the inhabiting *C. namaquensis*. Thus, colour lability precludes habitat background-matching, since it is pro-

tective only at colour indices of '2-3' at thermoneutrality. The complexity of colours in *C. namaquensis* is furthered by the individual variety in base ground colour and patterns, which is discussed in reproduction under sex determination and description of adult *Chamaeleo pumilus* and *C. namaquensis* (see p. 109). However, an individual chamaeleon can only change from light to dark, as Farghaly (1941) and others have noted.

The importance of radiant energy to ecological studies was emphasized by Gates (1962). All radiant heat energy reaching the earth is divisible into visible spectrum 40%, infra-red 40% and ultra-violet and radio regions 20%. As Norris (1967) emphasizes, complicating the assessment of radiation impinging on reptiles are such environmental factors as cloud cover, fog, surrounding vegetation, substrates and local topography. Since the skin of a reptile is its 'first line' of defence or adaption to usage and/or protection from such extraterrestrial emanations, it seems logical that colour lability serves as this shielding regulator. Radiant energy penetrating an organism may be important to lizards with a pigmented peritoneum, which may be significant in infra-red absorption. Thus, as Bartholomew & Tucker (1963) observed, changes in dermal radiative properties may help in thermoregulation.

Detailed studies of dermal colour lability as it relates to saurian ecology have been made to date only on American desert lizards, principally iguanids. Atsatt (1939) pioneered this investigation and others have expanded it. These are given in the reviews of Norris (1967) and Mayhew (1968).

Atsatt (1939) observed blanching in *Uta* at 22.0-25.0 C, but the upper level temperature (30.0 C) used did not produce blanching in the thermophilic *Dipsosaurus* because it only emerges (dark hued) at a minimum body temperature of 33.0 C, but becomes pale after warming to a foraging minimum of 38.0 C. Atsatt found that except for some *Callisaurus*, which are first pale then dark, all iguanids at low body temperatures have dispersed melanin, whereas at high temperatures relative to normal activity levels they assume the light condition. Between the extremes, temperature is not an overriding influence, and illumination tends to regulate melanin dispersal. In this middle thermal range lizards tend to become dark when placed in light and vice versa.

The grasshopper *Kosciuscola tristis* is black at 15 C; at temperatures greater than 25.0 C it is a bright greenish-blue, and intermediate shades between 15 and 25 C. Paling occurs two to three hours after sunrise, darkening again in late afternoon. Colour lability of this orthopteran seems thermoregulatory to lessen the heating effect of the midday sun (Fingerman 1965). Thermal colour lability in other invertebrates, especially intertidal crustaceans, is also discussed by Fingerman, harmonizing with that given for vertebrates.

Virtually all amphibians and reptiles disperse melanin at low temperatures and concentrate it at high temperatures, agreeing with a thermoregulatory role. Rivalling any colour labile reptile, the anuran *Hyla versicolor* is dark at 3.0-5.0 C, and lightens with increased temperature. Deanin & Steggerda (1948) have shown that a pale *Hyla* reflects more light, principally the heat-

producing longer wavelengths, than dark individuals. Cole (1943) demonstrated that dark-coloured reptiles more rapidly overheated than light-coloured ones.

Working with several reptiles, Krüger & Kern (1924) showed black in *Lacerta* serves for heat absorption and light filtering. Thus, quanta of light penetrating to the body cavity might harm tissues (this would be ultra-violet absorbed by DNA), but the skin effectively blocks this when melanin is dispersed. Hutchinson & Larimer (1960) confirmed Krüger & Kern's finding that melanin dispersed in the dermis blocks 80% of the radiation from penetrating the interior. Therefore, a warming lizard exposing itself to the sun can achieve warmth without harm. Mayhew (1968) reviews this problem of light penetrating the body cavity with pertinent references.

The role of the black abdominal peritoneum is often cited as the barrier to harmful light, but Hunsaker & Johnson (1959) found the outer skin the chief reflector of ultra-violet, mainly wavelengths of 187–310 m μ . Porter (1966) noted most earlier investigators used wavelengths atmospherically absorbed and not reaching the earth's surface. Therefore, he used wavelengths (290–2 600 m μ), comprising 97% of the solar energy reaching the earth. His results showed that the skin is the prime absorber of energy, followed by the muscles, and then by the black abdominal peritoneum. However, more ultra-violet than previously thought penetrates to the body cavity.

In *Chamaeleo namaquensis* there is a transparent abdominal peritoneum (Fig. 12), with black visceral peritoneum occurring on the digestive tract, save the stomach, and variously wholly, partly, or absent on the testes. Only the American deserticolous teiid *Cnemidophorus tigris* has a transparent abdominal peritoneum among other diurnal series, but this teiid is protected by a large, immobile deposit of melanin in the dermis. Warming *Chamaeleo namaquensis* would be protected from harm by a colour index of '5', but it is impossible to deduce how it protects itself when at the pale hues in the midday Namib Desert heat and high illumination, unless; 1) the transparent abdominal peritoneum has strong reflective capabilities (?); 2) the light phases of *Chamaeleo namaquensis* are more efficient in dermal reflectivity than has been previously recorded (Waring 1963; Norris 1967; Mayhew 1968). *Chamaeleo pumilus* has black abdominal and visceral peritoneum, which may wholly or partly cover the testes, rarely absent, and always shields the uterus. Mayhew (1968) notes that no lizard capable of marked colour change lacks a black abdominal peritoneum.

The previous discussion shows that warming reptiles expose themselves to light (=heat), and how they might protect themselves from the harmful effects of exposure to the sun; it reports dark phase (colour index '5') for warming *Chamaeleo pumilus* and *namaquensis*, light phase (colour indices '<2') for cooling individuals, and colour indices '2–3' for those at thermoneutrality. The same findings have been recorded for several American deserticolous iguanids, such as *Dipsosaurus*, *Holbrookia*, *Phrynosoma*, some *Sauromalus*, *Sceloporus*, *Uma*, and *Uta*, tropical *Anolis* (Ballinger *et al.* 1970), some gekkonids, several

agamids, for example, *Amphibolurus* (Bartholomew & Tucker 1963), and *Moloch* (Pianka & Pianka 1970), and even snakes, for example, the deserticolous *Crotalus cerastes* (Norris 1967).

Norris (1967) computes the net energy gain at lightest phase (71.2 cal/min) and darkest phase (92.4 cal/min) for *Dipsosaurus*, a deserticolous iguanid roughly the same size as *Chamaeleo namaquensis*. Norris concludes that colour change has value as a heat flux control for warming *Dipsosaurus*. The same seems true for *C. namaquensis* and *C. pumilus* as well as *Dipsosaurus*. As Norris points out, the desert environmental temperature, coupled with local topographic conditions can put desert species in the centre of a reflector oven, where, he feels, colour lability would be of minimal value. Here other adaptations might be of importance.

It is doubtful that forced convection from wind is of importance to cooling in *Chamaeleo namaquensis*, since this species was often observed active without discomfort in wind-protected areas between dunes in sizeable pockets of still air (i.e. a reflector oven). Also, light is very bright in the Namib Desert, particularly in the coastal dunes, with high reflection from the substrate. The air temperature at two metres and the heat load in a reflector oven are stultifying and the light dazzling, yet *C. namaquensis* seems quite at ease, pallid to the sun, patterned to the reverse, and always at a body compression index of 'IV'. *C. namaquensis* has a white venter, which undoubtedly reflects light and heat rebounding from the substrate. The venter pattern of *C. namaquensis* and *C. pumilus* is similar, differing only in colour, and consists of a broad mid-ventral white or dusky-white band edged by a narrow, conspicuous band of light gray in *C. namaquensis*, greenish in *C. pumilus*, dorsal to which white resumes up to the main laterum colour. Reflection from the venter can be cancelled by adpression (compression index 'I') to the substrate. Although most reflectivity data answer problems of colour lability and thermoregulation for *C. pumilus* and *C. namaquensis*, the problems of a transparent abdominal peritoneum, and the reflective efficiency of the light phases of the latter yet remain. *C. namaquensis* inhabits areas devoid of vegetation, and rarely seeks relief in shade where shelter is present.

Some workers (Mayhew 1968) see colour as wholly, or chiefly for protective concealment (Schmidt-Nielsen & Dawson 1964). As Norris (1967) points out, best matching (see previous discussion p. 56) occurs at thermoneutrality. This is what Klauber (1939) was considering, actually predicting many findings made later, and he is not a proponent of colour being primarily for concealment. Norris (1967) and the author feel that if a dark-hued animal is not concealed while warming (cf. *Chamaeleo pumilus* and *C. namaquensis*), the rate of warming must be rapid (Table 8), so that thermoneutrality brings concealment coloration. *C. namaquensis* follows this, so it can be said that diurnal deserticolous species are generally conspicuous on pale habitats (cf. the permanently black Pisgah *Uta* reported by Norris 1967) when black during warming, but quickly gain concealment with paler hues at thermoneutrality and cooling. Thus, pale for thermoregulation and concealment are synergistic at high environmental temperatures.

Unfortunately, no data are available to compare *Chamaeleo pumilus* with non-desertic or 'temperate' colour labile forms, but it can be said that *C. pumilus*, subjected to prolonged cool environmental temperatures, is concealed best while warming at a colour index of '5' (reverse of desertic lizards) and at thermoneutrality, and quite conspicuous at the palest hues.

9. *Summation of chamaeleon thermoregulation in comparison with other reptiles; role of posture*

Body compression and associated colour lability in thermoregulating *Chamaeleo pumilus* and *C. namaquensis* are discussed in detail on pages 42-7. Body compression 'I' gives chamaeleons an ellipsoid shape in cross-section, increasing surface area by 30% and body width by 33,3%. The surface area of the back is especially increased, acquiring the outline of a large sphere. (See Norris (1967) for the value of this.) This posture, in adpression to the substrate minimizes convective heat loss, and concentrates initial warming on the mid-dorsum. Heating is exaggerated on the lungs of both chamaeleons and the air sacs of *C. namaquensis*, which lie close to the dorsum when inflated, and also on the dorsal aorta. The essentially body compression 'II' is considered the 'normal' body form and is a posture at thermoneutrality. The slightly laterally compressed body compression 'III' which only reduces body width by 10% is the other posture at thermoneutrality. Body compression 'IV' reduces body width by 30%, and increases the total surface area by at least 110%. Fine orientation increases or decreases the intensity of impinging insolation, such as the longitudinal axis presented with the head to the sun with the light striking on both sides of the chamaeleon's body; lateral body compression with the centre of one side directly facing the sun, or slanted so the sun obliquely hits that side. Frequently the chamaeleons tilted, so both sides received the sun, concentrated on the dorsum.

Body compression, mostly dorso-lateral flattening, has been recorded for various forms, for example, *Anolis* (Ballinger *et al.* 1970), *Amphibolurus*, *Sauromalus* and *Crotalus* (Norris 1967), and *Uta* (Burrage 1966). Heath (1962a) found that *Phrynosoma* facing into the sun achieves a more reduced heat load than when in the opposite position. Greatest heat load is when the lizard presents itself broadside to the sun.

Lillywhite (1970) demonstrated behavioural thermoregulation in the anuran *Rana catesbeiana*. By postural adjustments, this frog maintains active body temperatures of 26,0 to 33,0 C (\bar{x} =30,0 C), using pond water as a heat source or sink. Body temperatures of these frogs closely followed that of the dry bulb air temperature.

10. *Summation of chamaeleon thermoregulation in comparison with other reptiles; roles of the lungs, the cardiovascular system and temperature control centres*

Previously, lungs do not seem to have been considered as thermoregulatory aids in reptiles and information on this is circumstantial, since no probes were

inserted into the lungs or air sacs of the chamaeleons. As stated, the air sacs of *Chamaeleo namaquensis* were pumped and held full during warming, and alternately filled and flushed in cooling. The distal parts of the lungs in *C. pumilus* acted as air sacs. Tornier (1904) made an exhaustive study on chamaeleon air sacs, including those located in the gular and occipital regions, which possibly aid in maintaining cranial thermo-homeostasis. Tornier showed that the air sacs are valved to regulate the passage of air, which is shunted in and held. He showed their value in puffing-up in defence, which this study endorses. However, the distal parts of the lungs of *C. pumilus* and *C. namaquensis* and the air sacs of the latter serve as dead air spaces, which when full and closely adpressed to the body wall could act as temperature stabilizers or reservoirs, maintaining even temperatures or insulation from high temperatures for the reproductive organs and other vitals to which they are closely adpressed (Fig. 12). Body compression increases the surface area of the lungs and air sacs. Couvreur & Gautier (1904) found a distinctly thermally correlated respiratory pattern in *C. chamaeleon*, involving flushing of the air sacs at 42.0 C.

Bakker (1971), in his paper on the probable physiology of dinosaurs and other archosaurians, postulates that chamaeleonids may use their lungs and air sacs in thermoregulation and/or for protecting their gonads. It seems that this suggestion is valid.

It could be assumed that chamaeleonids are not alone in using their lungs for thermoregulation, and that *Varanus* similarly uses its lungs. The lungs in *Varanus* are large, as in the chamaeleonids, and occupy a large part of the thoracic cavity, closely applied to the dorsal surface of the body cavity. When warming, *Varanus* flattens in the sun and laterally expands, increasing the surface area of the lungs. Since many reptiles do likewise, the role of the lungs in thermoregulation may be widespread.

The peculiar anatomy of the squamate heart (White 1959) and great vessels consists of a ventricle imperfectly divided into dorsal and ventral chambers. The ventricular base communicates with the atria, the right and left systemic arches and the pulmonary artery. The systemic arches join symmetrically, forming the dorsal aorta just posterior to the heart. The right systemic arch is the only supply to the head and anterior parts, other than a small connection from the left arch. This arrangement could favour a device for increased cardiac output for heat transport by allowing large volumes of venous blood to bypass pulmonary resistance. Concurrently, well-oxygenated blood could be supplied to the brain via the right systemic arch. Cardiac output could increase beyond the need for respiratory exchange without the energy expense to pass the whole cardiac output through the pulmonary circuit and without cutting the oxygen supply to the brain. The incomplete ventricular septum hypothetically could allow venous blood to exit directly via the left systemic arch and continue to the posterior parts of the body. Experimental data (White 1959; Tucker 1966; Baker & White 1970) have shown that the blood in the left systemic arch has an oxygen content equal to or somewhat less

than that of the blood in the right systemic arch, but not vice versa, agreeing with the hypothesis that this arrangement could be of thermoregulatory value.

Thus, in warming, an open pulmonary circuit, with high systemic resistance, favours a cardiac left-right shunt, increasing the pulmonary blood supply for warming, with a well-oxygenated blood supply to the brain and major sense organs via the right systemic arch. When warming is completed the increase of pulmonary resistance would invoke a proper double circulation. Increase of this resistance would result in a systemic arch circulation, thus enabling the reptile to conserve heat through toleration of high anoxia in the posterior trunk. (See Gordon, Bartholomew, Grinnell, Jorgensen & White (1968) and Tucker (1967) for a discussion of reptile circulation, respiration and temperature control centres.)

An efficient peripheral vascular circulatory arrangement, involving shunts, is necessary for dermal heat absorption or reflection to have any importance in body temperatures. Cowles (1958) pointed to the importance of dermal temperature regulation in the development of endothermy. His elaborate experiments showed that lizards in fur coats benefited from insulation only when warmed. According to Cowles, in amphibians the vascularized dermis serves chiefly in respiration, but possibly the dermis also had a thermoregulatory function in extinct terrestrial labyrinthodonts. In reptiles the dermis serves in thermoregulation. In the truly endothermic birds and mammals the dermis functions in thermoregulation with fur or feathers for insulation.

Experimentally, Cowles (1958) demonstrated in *Dipsosaurus dorsalis* a temperature gradient is greatest during heat absorption; not so in cool air. Subdermally injected water blebs heated on one side only, showing that the heat is more rapidly dispersed on the radiated side, heat being transferred to the body interior in warming lizards. The dermal vascular supply was greater at higher warming temperatures. Trying Cowles's method with *Chamaeleo pumilus* and *C. namaquensis* yielded equivalent results, and at high temperatures the blebs were cooler on the radiated surface, indicating cooling. In cooling (pallid) chamaeleons, there was no gain in bleb temperature, indicating peripheral dermal vasomotor control, which may be mediated by the change of pigment dispersal itself. A lizard being cooled constricts peripheral circulation to preserve body core heat—as does one resting at night, and dilation of peripheral circulation upon basking allows a warmth exchange with the interior.

Bartholomew (1966), Bartholomew & Tucker (1963, 1964), Bartholomew, *et al.* (1965) and Weathers (1970) report representatives of the Agamidae, Iguanidae, Scincidae, Gekkonidae, and Varanidae heat faster than they cool. Some of these differences are attributable to endogenous heat production and circulatory adjustments. The degree of circulatory control of heat transport varies. In the agamid *Amphibolurus barbatus* 75% of the difference in heating and cooling is assignable to circulatory changes, but in the skink *Tiliqua scincoides* this difference is due to endogenous heat production. Varanids are intermediate. Much the same situation is seen in the marine iguanid *Ambly-*

rhynchus cristatus (Bartholomew & Lasiewski 1965). In the sea the cardiac rate drops and the peripheral vessels are constricted, with tolerance of anoxia in the body tissues, especially when diving. Basking on land, the peripheral vessels dilate as the cardiac rate increases. Thus, it should be emphasized that an increased cardiac rate and/or vascular bed adjustments are important in this process.

Heath (1962a, 1964a, b, 1965, 1966) has demonstrated differential head-body temperatures of as much as 3 C to 5 C in partly buried *Phrynosoma*, and De Witt (1963, 1967a) found this to be true also for *Dipsosaurus dorsalis*. Bruner (1907) describes sphincter muscles around the internal jugular veins. Contraction of these muscles reduces the flow of blood from the head. Closure of the internal jugular veins accompanies an increased heat flux from the head to the body in *Phrynosoma*, which Heath (1963) feels may be important in the thermoregulation of these lizards. Dissection revealed sinuses in the head of both *Chamaeleo pumilus* and *C. namaquensis*, but their functional significance was not investigated; they may possibly serve as in *Phrynosoma* and *Dipsosaurus*. Such a cranial circulation, as with peripheral circulation, would involve shunts.

Sensitivity of some centre is required to mediate reptile body temperatures to stability through use of the physiological methods discussed. Adams (1957) showed that chamaeleons possess a carotid body, very similar to that of mammals, which mediates blood pressure by increasing and decreasing stroke volume. The nature of the chamaeleon carotid body, the peculiarity of the chamaeleon lungs and air sacs, the nature of the squamate heart and great vessels, and the peripheral and cranial vascular supply would suggest a role of the cardiovascular system in thermoregulation.

Hammel, Caldwell & Abrams (1967) and Cabanac, Hammel & Hardy (1967) showed for the skink *Tiliqua scincoides* a thermally responsive (3 cold neurons, 5 warm—heat sensitive) region in the preoptic part of the brain. Heating or cooling the brain stem resulted in the appropriate behavioural thermoregulation for stabilization, but prematurely at higher or lower temperatures than normal. However, dermal and body temperatures also impinge on thermoregulation in this species. Saalfeld (1936) found similar thermal receptors in the medulla of lizards. Rodbard (1948), Rodbard, Sampson & Ferguson (1950) and Heath, Gasdor & Northcutt (1968) made similar findings for turtles.

This study records panting in *Chamaeleo pumilus* and *C. namaquensis*. Templeton (1960) showed for *Dipsosaurus dorsalis* and Dawson & Templeton (1963) for *Crotaphytus collaris* that panting dissipates 1.3 times the metabolic heat production at 44.0 C and felt the water loss negligible. *Chamaeleo pumilus* and *C. namaquensis* can easily maintain their water requirements, so this method of cooling could be most effective for them. Panting is recorded in several lizards (Dawson 1967; Mayhew 1968), except those that are not heat-resistant (e.g. *Eumeces obsoletus*), who pant weakly, or not at all, even under thermal stress. Varanids have a strong gular pumping action at high temperatures. Panting

ensues close to the maximum voluntary body temperature, except in *Chamaeleo namaquensis* in which it begins early (see p. 47). Richards (1970), in a detailed review of panting, concludes that it is an ancient method, and true endothermy may have originated as a response to dissipating endogenous heat in hot environments.

11. Oxygen consumption

Table 16 shows oxygen consumption, breathing rate, and Q_{10} for *Chamaeleo pumilus* and *C. namaquensis* at rest and activity. Peak oxygen consumption was at 25 C for *C. pumilus* and at 35 C for *C. namaquensis*. The large increase in oxygen consumption for *C. pumilus* at 40 C was a reflection of the frenzied escape activities of the subjects at this temperature, and is so out of pattern and based on such few frantically active individuals that it might be advisable to ignore it. This seems odd, since *C. pumilus* was encountered in the field at environmental temperatures of nearly 40 C, but had a lower body temperature, perhaps assignable to the ease of thermoregulating in nature which they could not properly undertake in the oxygen consumption chamber. Except for those *C. pumilus* at 40 C, both species showed a reduction in oxygen consumption past their thermal preferendum. There was an apparent temperature difference in oxygen consumption between coastal and inland *C. namaquensis*, though they are reported here as a unit.

Literature reviews of the oxygen consumption of lizards are given by Dawson (1967), Tucker (1967) and Mayhew (1968). In the thermophilic *Cnemidophorus tigris* (teiid), and the less heat-resistant *Gerrhonotus multicarinatus* (anguid) and *Coleonyx variegatus* (eublepharid) the Q_{10} remains constant over at least 20 C, including low temperatures (Dawson 1967), but in the thermophilic iguanids *Crotaphytus collaris*, *Dipsosaurus dorsalis* and *Uma notata*, and the less heat-resistant xantusiid *Xantusia vigilis*, the Q_{10} varies with temperature, usually decreasing as the animals become warmer (Cook 1949; Dawson & Bartholomew 1958; Dawson & Templeton 1963). The equivalent-sized *Dipsosaurus dorsalis* and *Crotaphytus collaris* have lower resting metabolic rates between 35–40 C than the less heat-resistant skink *Eumeces obsoletus* (Dawson 1960) and *Gerrhonotus multicarinatus* (Dawson & Templeton, unpublished data, see Dawson 1967), possibly because the first pair have lower oxygen requirements at high body temperatures. Below 15 C the heat-resistant forms show somewhat higher values than those that are less heat-resistant, indicating some cold sensitivity of the former.

Mayhew (1965) found in *Phrynosoma m'calli* (iguana) oxygen consumption increased until 35 C, with a metabolic plateau at 35–40 C and a marked increase resumed at 45 C. He sometimes found quite a difference in oxygen consumption of laboratory and field measurements, though recorded under apparently identical conditions. Bullock (1955) noted that such metabolic plateaus are not unusual. Schmidt-Nielsen, Crawford & Bentley (1966) record the iguanid *Sauromalus obesus* to have continuous oxygen consumption curves,

Table 16

Oxygen consumption, respiration rates, and Q^{10} of resting and active *Chamaeleo pumilus* ($N = 15$) and *C. namaquensis* ($N = 15$) at various temperatures. (Means are shown in parentheses.)

<i>Chamaeleo namaquensis</i>					<i>Chamaeleo pumilus</i>				
Temp. °C	O ₂ consumption ml/O ₂ /gm/hr**	Active		Q^{10}	O ₂ consumption ml/O ₂ /gm/hr**	Active		Q^{10}	
		Range	Respirations per minute			Range	Respirations per minute		
5	not active at 5°C								
15	0,12-0,16 (0,15)	4-10	(7,0)	15-25 C	0,18-0,9 (0,41)	4-12	(8,2)	5-15 C	
25	0,12-0,44 (0,22)	5-18	(10,8)	1,47	0,25-0,97 (0,53)	10-15	(12,5)	1,29	
35	0,17-0,81 (0,64)	18-38	(26,1)	25-35 C	0,45-0,99 (0,67)	10-19	(15,3)	15-25 C	
40	0,23-0,86 (0,57)	60-90	(85,0)	2,91	0,29-0,9 (0,55)	15-35	(25,5)	1,26	
45	0,31-0,73 (0,42)	80-+100 (+90,0)*		35-45 C	1,11-1,9 (1,31)	+100*		25-35 C	
				0,64		no record			
5	0,02-0,06 (0,04)	0,03- 0,9	(0,3)	5-15 C	0,03-0,06 (0,05)	0,7- 2,0	(1,4)	5-15 C	
15	0,03-0,09 (0,05)	0,1- 3,0	(1,1)	1,25	0,05-0,08 (0,06)	5,0- 7,0	(6,0)	1,2	
25	0,03-0,09 (0,06)	0,7- 8,0	(4,0)	15-25 C	0,06-0,12 (0,10)	6,0-14,0	(7,0)	15-25 C	
35	0,06-0,12 (0,10)	5,0- 9,0	(7,3)	1,2	0,08-0,13 (0,12)	6,0-11,0	(8,0)	1,67	
40	0,06-0,14 (0,11)	20,0-24,0	(22,0)	25-35 C	no record			25-35 C	
45	0,12-0,18 (0,17)	30,0-36,0	(33,0)	1,67	no record				
				35-45 C					
				1,7					

* Rate was too rapid for an accurate count.

** Corrected to standard temperature (0°C) and pressure (760 mm Hg).

but some had periodic peaks interrupted by periods of no detectable oxygen consumption, with a highly variable oxygen concentration of the air in the lungs.

Resting *Chamaeleo pumilus* showed a gradual increase in the Q_{10} of oxygen consumption values up to their thermal preferendum, but between 25–35 C the Q_{10} dropped to the same level (1,20) as that from 5–15 C. Resting *C. namaquensis* oxygen consumption Q_{10} values were variable, though generally increasing with temperature. The Q_{10} values of both these species of chamaeleons suggest they are in the less heat-resistant category of lizards.

In maximally active lizards Bartholomew & Tucker (1963) showed the Q_{10} of oxygen consumption in the agamid *Amphibolurus barbatus* to increase rapidly between 15–20 C, but to decrease thereafter. In *Varanus* spp. (Bartholomew & Tucker 1964) and the skink *Tiliqua scincoides* (Bartholomew *et al.* 1965) the maximal rates of oxygen consumption at various temperatures have a constant Q_{10} between 20–40 C, which are lower than the corresponding ones for resting animals. *Iguana iguana* between 15–30 C shows an active Q_{10} exceeding that for resting individuals. Active *Chamaeleo pumilus* had the greatest Q_{10} value (1,29) for oxygen consumption over 5–15 C, dropping slightly (1,26) over 15–25 C within the thermal preferendum of this species, thereafter dropping sharply. Oxygen consumption of active *C. namaquensis* had a Q_{10} of 1,47 between 15–25 C, with the greatest Q_{10} value (2,91) between 25–35 C within the thermal preferendum of this species, dropping very sharply (0,64) thereafter. *C. pumilus* and *C. namaquensis* active Q_{10} values were greater than those for resting individuals, except for the respective values at 25–35 C (*C. pumilus*) and 35–45 C (*C. namaquensis*) when the reverse was true.

Measurements of metabolic rates of maximally active and resting lizards may indicate the available energy to them for activity at various temperatures ('scope for activity' of Fry 1947). Moberly (1964) notes that this is complicated by indications that these animals rely extensively on anaerobic metabolism during activity, so oxygen consumption measurements may not give the full extent of energy utilization. Schmidt-Nielsen, Crawford & Bentley (1966) report continuous oxygen curves for *Sauromalus obesus* (iguanaid), but other curves had periodic peaks interspersed with periods when no oxygen consumption was detectable. The same phenomenon was observed in *C. pumilus* and *C. namaquensis*. Aerobic scope for activity is maximal at 20 C for *Amphibolurus barbatus*, approximately 15 C below the activity temperature and thermal preferendum of this species. *Iguana iguana* has its maximum aerobic scope for activity at about 31 C; five degrees below its activity temperature. But in *Varanus* spp. with activity temperatures between 35,5–37,1 C and *Tiliqua scincoides* with an activity temperature of 32,6 C, the aerobic scope for activity increases with temperature between 20–40 C.

Without comparative data for other chamaeleonids, generalizations of data for *Chamaeleo pumilus* and *C. namaquensis* to that for other lizards have little meaning. All lizards discussed in the above paragraph were stimulated to

maximal activity by electric shocks. Since chamaeleons struggled ceaselessly, electric shocks seemed unnecessary. *C. pumilus* appeared, however, to follow the pattern of *Amphibolurus barbatus*, whereas the greatest aerobic scope for activity of *Chamaeleo namaquensis* was at its thermal preferendum, which may corroborate its ability to stabilize its body temperature by the physiological methods discussed elsewhere. The slightly higher Q_{10} of *C. pumilus* between 5–15 °C indicates its ability to be active at low temperatures.

Water loss in respiration is discussed in the section on 'Water and salt balance', and further remarks on metabolism are given in the section on 'Food habits'.

12. Activity patterns: daily and seasonal

Chamaeleo pumilus and *C. namaquensis* emerged from overnight spots independent of weather in all seasons. To be sure, prolonged days of rain discouraged *C. pumilus* activity in the open, but it was active within dense vegetation, which afforded shelter from heavy, driving rain, and probably more importantly from strong accompanying winds. Soft rain and occasional intermittent showers had no marked effect on discouraging activity in the open. In fair, or cloudy weather *C. pumilus* spent the night in exposed conditions, so that the first rays of the rising sun struck them early. Thus, *C. pumilus* was active as early as one hour before sunrise. This was particularly true of 'Fair Warm' days, though it must be remembered that the environmental temperature ($T_{a50\text{ mm}}$) was often quite warm. A daily minimum in summer of 11.5 °C ($T_{a2\text{ m}}$) was recorded, and a summer minimum as low as 6.0 °C has been officially recorded.

The daily temperature regimens of *C. pumilus* are given in Table 17. Cloud cover of 30% or more was considered overcast, since at that minimum coverage alteration of environmental temperatures was noted. Inspection of the data for 'Cool Cloud' and 'Cool Rain' show chamaeleon body temperatures to be higher than environmental temperatures. And as previously emphasized, high chamaeleon body temperatures were not necessarily recorded with high environmental temperatures. Details of heat maintenance are given in the thermoregulation: warming/cooling section (pp. 42–7). Excessive heat was not a problem for *C. pumilus*, since it mitigated this by resorting to shade.

C. pumilus retired for the night at paler hues and with body temperatures higher than those at emergence. This was about the same time as sunset. Retiring with paler hues may be an effect of insufficient light intensity to excite melanin dispersal, as Cleworth's (unpublished data) experiments indicate. Dermal heat exchange is reduced by a lower heart beat and peripheral vasoconstriction would conserve body core heat by reducing the blood flow to the periphery.

Chamaeleo namaquensis spent the night in various shelters, such as burrows, rock crevices, in thick vegetation, and sometimes in the open. Those not in burrows always ended their daily activity in the shade away from the setting sun to the lee of some object. This strange behaviour proved as 'correct' as

C. pumilus settling down in exposed sites, since both methods afforded access to the first rays of the rising sun on the following morning. The previous remarks for *C. pumilus* upon retiring are also applicable to *C. namaquensis*, except of a night when the latter goes into a full torpor from which it was very difficult to arouse.

Body temperature data for *Chamaeleo namaquensis* are in Table 17. Overcast criteria are as for *C. pumilus*. But it should be noted that fog was the usual overcast type for *C. namaquensis*, especially coastal populations, for which no distinction is made for drizzle, the rare event of rain, or whether the fog was down to the ground or at what altitude.

Of note was the stability and often narrow range of *C. namaquensis* body temperatures after initial warming, as compared to that of the environmental temperatures, regardless of the population considered. Highest and lowest environmental temperatures were recorded at the coast.

There is no inland record for 'Cool Overcast'. The substrate in 'Cool' months heats almost to as great (48,5 C) a maximum as it does in 'Warm' months (58,0 C), though the corresponding maximum body temperature records at these readings were 39,7 C ('Cool'), and 37,0 C ('Warm'). 'Warm Overcast' has maximum environmental temperatures eight degrees cooler than 'Warm Fair'.

Coastal populations were subjected to more varied environmental temperatures than those recorded at inland locales. Coastal 'Cool Overcast' environmental temperatures were as low as 8,0 C, and the coastal 'Warm Fair' maximum environmental temperature was 67,0 C. The body temperatures of active *C. namaquensis*, subject to these environmental temperatures, were 14,0 C and 34,2 C, respectively. For 'Partly Cloudy' conditions, the clearing of the fog was reflected in a sudden increase of the environmental temperatures, whereas the environmental temperatures drop upon the return of the fog. Of especial note with both *C. namaquensis* populations was the rapid increase in warming body temperatures in the early part of the day and the stability and narrow body temperature range independent of the environmental temperature throughout the bulk of the day. So, too, towards the end of the day body temperatures stabilized, even slightly rose, or declined very little in comparison with the rapidly dropping environmental temperature. Wind intensity has no effect on the activity of *C. namaquensis*. The thermal qualities of the surface of the substrate are discussed in the relevant section on habitats (pp. 28-9), and at depths in Table 45 in the discussion of incubation in the section on reproduction (see p. 115).

First daily order of business of *Chamaeleo pumilus* and *C. namaquensis* was basking (= warming), which upon their body temperatures reaching minimum operating levels (3,5 C *C. pumilus*; 14,0 C *C. namaquensis*), defecation, drinking, feeding and courting (see Behaviour, p. 72) usually followed. The previous arrangement is not meant to imply that this was the order followed, since neither chamaeleon was averse to forgoing drinking for a delectable prey item,

Table 17

Summary of environmental and body temperature (in degrees Celsius) relationships of 549 active *Chamaeleo pumilus* at Cape localities only, mostly Stellenbosch and vicinity, and 351 active *C. namaquensis* in the Namib Desert on the coast, mostly Swakopmund and vicinity, and inland, mostly Gobabeb and vicinity throughout the day in cool (April–September) and warm (October–March) months during daily weather conditions of; fair (0–29% cloud), rainy, overcast (30–100% cloud), and partly cloudy, referring to early morning and late afternoon fog in the coastal Namib.

Locality	Season	Condition	N	Body temperatures		Air temperatures 2 m		Environmental temperatures	
				Range	Mean median	Range	Mean median	Range	Mean median
Cape	<i>C. pumilus</i>								
	cool	fair	97	3.5–30.1	19.9	22.5	18.3	2.0–30.1	17.0
	"	overcast	84	11.0–29.8	20.6	21.0	15.6	4.0–27.5	16.3
	"	rain	60	12.8–24.2	18.4	18.3	14.6	7.7–21.0	13.9
	warm	fair	137	17.0–37.0	28.1	28.5	25.4	15.0–39.0	25.2
	"	overcast	88	14.0–30.0	24.3	26.0	20.4	13.0–29.0	20.0
Inland	<i>C. namaquensis</i>	rain	83	13.5–34.8	22.8	23.0	18.4	12.0–27.5	18.4
	cool	fair	34	15.0–39.7	29.9	33.3	25.2	11.0–48.5	30.8
	"	overcast	28	20.0–39.0	29.0	30.0	23.1	18.0–50.0	33.6
	warm	fair	28	26.0–37.9	32.0	31.5	27.2	26.0–58.0	41.0
	cool	overcast	31	14.0–29.0	21.9	22.0	13.2	8.0–28.0	18.4
	"	partly cloudy	43	14.2–36.2	26.8	28.5	17.6	8.0–55.0	24.0
	"	fair	51	14.5–31.0	27.3	28.3	14.4	8.0–47.0	21.3
	"	overcast	39	17.5–35.4	27.7	27.8	18.1	14.2–33.9	23.5
	warm	partly cloudy	51	14.0–31.0	27.3	28.8	20.7	18.0–54.5	32.6
	"	fair	45	23.4–34.2	30.9	31.1	21.1	18.0–67.0	38.4

N.B. See page 10 for environmental temperatures of *C. pumilus* and *C. namaquensis*.

an attractive mate, or repelling an invader. Also, some items are performed concurrently. *C. pumilus* frequently resorted to 'emergence' warming basking on cold or inclement days, though *C. namaquensis* rarely did so, even in drizzle and strong wind, though it did turn black (colour index '5') and assumed body compression index 'IV'. So, too, *C. namaquensis* (pallid to the sun, patterned on the side in the shade) was abroad during midday heat on the hottest days, though it would be hard put to find shade in such localities as the featureless gravel plains.

Chamaeleons appear to be wholly diurnal, as Uible (1968), Rosen (1950) and Spence (1966) report for those in the field, and Bustard (1965, 1966) and Von Frisch (1962) record for captives. In captivity chamaeleons kept pretty much to their wild regimen, but some captive *C. pumilus* and *C. namaquensis* were not averse to eating at night if illumination was provided. The exception was for captive females excavating nests, which is discussed further in the section on reproduction (p. 114).

Details of daily and seasonal activity for other diurnal saurians can be consulted in Mayhew (1968) for comparison with *Chamaeleo pumilus* and *C. namaquensis*. Excluding brumating species, as a rule seasonal changes include later daily emergence and earlier retreat in the cooler months, taking into account the effect of sunrise and sunset. Heath (1962*a, b*) records temperature-independent emergence in the iguanid *Phrynosoma*. Burrage (1966) found that different substrates have different thermal gradients and that this controls emergence in the iguanid *Uta stansburiana hesperis*, regardless of the weather. 'Normal' emergence, though, is about sunrise, or its equivalent. Ground fog has a delaying effect on *uta* emergence, but high thin fogs and no wind favour a 'greenhouse effect', aiding substrate heating. These emergent control factors are also noted in another iguanid, *Sceloporus orcutti* (Mayhew 1962), and the teiids *Cnemidophorus sexlineatus* (Fitch 1958; Hardy 1962), *C. sacki*, *C. perplexus*, *C. tessellatus* and *C. tigris* (Milstead 1957). The daily order of business and retreat time for most other saurians is as described for chamaeleons, but *Uta stansburiana* is active up to an hour after sunset (Irwin 1965; Burrage 1966) as is *Urosaurus* (Shaw 1950).

Midday increase in substrate temperatures and wind intensity are generally regarded as forcing saurians into retreats (Tinkle 1967, and Irwin 1965, for *Uta stansburiana stejnegeri*; Milstead 1957, for *Cnemidophorus perplexus*, *C. sacki*, *C. tessellatus* and *C. tigris*; and Bostic 1964, for *Cnemidophorus hyperythrus*). These factors do indeed have some correlation, especially for winds greater than 9.3 kph. But, as Burrage (1966) reports for *Uta stansburiana hesperis*, this may not be true on closer inspection, as utas are quite abundantly active under open vegetation, where the effect of wind is lessened and cooler substrates are found. Also, wind effect may be indirect, since utas restrict their activity to wind-protected sites because their prey are limited to such situations. Thus, the lizards go under open vegetation to find their prey in a concentrated and perhaps more vulnerable situation. *Chamaeleo pumilus* in intensifying wind some-

times restricted its activity to plant cover, because the flying insects which form its main prey were restricted to protecting vegetation by strong winds. *Chamaeleo namaquensis* was active in the strongest winds with blowing sand in the air and small gravel blown along the ground. Under such conditions, its prey was also abroad, even in winds strong enough to upset beetles and small lizards, such as *Eremias*.

G. Behaviour

1. Senses

Most studies of the senses of chamaeleons focus on their highly developed visual acuity, and it seems strange that the auditory organ should either not have developed (Hamilton 1960; Schmidt 1964) or degenerated (Miller 1966). While the auditory apparatus of chamaeleons is unique, the chamaeleonid cochlear duct could result from regression of the agamid type (Miller 1966). Only six of the 100-odd chamaeleon species have been studied: *Chamaeleo vulgaris* (= *C. chamaeleon*) by Versluys (1898) and Parker (1880); *Microsaura pumila* (= *C. pumilus*) by Parker (1880), Engelbrecht (1951) and Toerien (1963); *Lophosaura ventralis* (= *C. pumilus*) by Brock (1940); *Chamaeleo senegalensis* and *C. quilensis* by Wever (1968); *Brookesia marshallii* by Toerien (1963); *B. supercilialis* by Siebenrock (1893); *Rhampholeon platyceps* by Frank (1951) and Toerien (1963). The two common features of the auditory apparatus of those chamaeleons examined (see also detailed summary of Baird 1970) consists of: no tympanic membrane; fenestra ovalis very small, or absent. Other variations and details in the previously mentioned species can be had by consulting the preceding sources.

Anatomically, it appears that *Chamaeleo pumilus* would be deaf to air-borne sounds. Blindfolded individuals did not respond to the shaking of a pebble-filled can nearby, nor to a rock impacting on the ground. They did respond to something hitting a branch, but this could also be tactile. Wever (1968) showed that *C. senegalensis* and *C. quilensis* have a poor auditory sensitivity in comparison to other lizards, yet not far below that in many species with a conventional auditory apparatus. Wever (1968) found *C. senegalensis* and *C. quilensis* to have a frequency range extending from 100 to 10 000 cycles per second, with best sensitivity in the region of 200 to 600 cps. Blindfolded *C. namaquensis* were very alert to ground-borne sounds, as a rock dropped on sand, and particularly on a rocky or gravel surface. Shaking a pebble-filled can nearby caused them to turn and hiss in its direction.

The sight of chamaeleons is almost a legend in zoology. Excellent discussions of the chamaeleon eye and the host of pertinent literature are given by Johnson (1927), Walls (1942), Polyak (1957) and Underwood (1970). Polyak's account of vision in vertebrates is most valuable, noting the same chamaeleonid-type eye mobility and perhaps visual acuity in the American iguanid *Anolis carolinensis*, with binocular stereoscopy in this and several other forms. The more chamaeleonid-like *Chamaeleolis chamaeleontides* is an even more

perfect duplicate (Wilson 1957). In *Anolis*, Polyak (1957) describes a 'sighting groove', a black area of decreasing width anteriorad, running from the anterior margin of the eye to the tip of the nose, which also occurs in esocid fish, among others. In the chamaeleonids this sighting groove is structural, rather than pigmented. It is widely stated in the literature that the chamaeleon eye is of 'unerring accuracy', and completely dependent on the functioning of both eyes. This study showed that nothing was further from the truth; especially in the latter instance.

Normal *Chamaeleo namaquensis* had an accuracy of 80 to 90% ($\bar{x} = 85,0\%$), but was usually a painstaking aimer, sighting at an object, positioning back and forth, and even taking sightings from different angles. *C. pumilus* and *C. namaquensis* often shot at moving prey, which conflicts with what Von Frisch (1962) notes for the former. Normal *C. pumilus* also tended to shoot with far less preliminaries and was accurate 75 to 92% ($\bar{x} = 86,0\%$) of the time. Discounting those temporarily blinded by the stings and bites of captured prey, several *C. pumilus* were found with only one functional eye. While the extent of this partial vision disability varied between individuals, some had one eye completely ripped out. These chamaeleons with only one functional eye had an accuracy of 57–63% ($\bar{x} = 60,0\%$). They aimed by fixing their sole eye on the target and slowly turned the head to face the target before shooting out their tongue. Adhesive tape on one eye was used to experimentally blind twelve each of *C. pumilus* and *C. namaquensis*; they were then allowed 24 hours' acclimatization. The chamaeleons were then given five daily trials at prey, all scoring zero on the first test day. By the close of the second day, the accuracy of both species was 15 to 30% ($\bar{x} = 22,7\%$), by the end of the third day, 45 to 55% ($\bar{x} = 50,1\%$), and by the end of the fourth day, 57 to 62% ($\bar{x} = 59,0\%$). They aimed in the previously described manner of naturally partly blind *C. pumilus*. If initially the left eye had been experimentally covered, there was no change in fourth day individual accuracy if the right eye was subsequently covered on the fifth day.

Of all squamates, Jacobson's organ is least developed in the chamaeleonids, and it may be reduced to a small pit without a mushroom body, as in *Microsaura pumila* (= *Chamaeleo pumilus*) (Malan 1946; Engelbrecht 1951), or absent in *Rhampholeon* (Frank 1951). Haas (1947) feels it is debatable as to whether Jacobson's organ has any sensory function in the chamaeleonids (Parsons 1970).

2. Defence

Chamaeleons habitually select a site as a retreat for the night, as is recorded for *Chamaeleo dilepis* (Wager 1958; Brain 1961), *Microsaurus pumilus* (= *C. pumilus*) of Von Frisch (1962), and *Microsaura damarana* (= *C. pumilus*) of Spence (1966), *Chamaeleo pardalis* (Bourgat 1968b), *C. jacksoni* (Bustard 1958), *C. hohnelii* (Bustard 1965) and *C. bitaeniatus* (Bustard 1966). In the case of arboreal forms, this is a favoured perch on a twig. While this was true of *C. pumilus*, in heavy rains it would climb to the underside of a large leaf and

in its manner of gripping it, create a satisfactory umbrella.

Both sexes of *C. namaquensis*, in the field and in captivity, occasionally constructed burrows for retreats. While some were undoubtedly abandoned small rodent burrows, others were purposely dug by the chamaeleons. They were less elaborate than a nest burrow (see reproduction, p. 114). A retreat burrow constructed by a male 90 mm snout-vent, consisted of a terminal chamber 95 mm long, 63 mm wide, and 38 mm from the floor to the ceiling. The roof of the terminal chamber was 75 mm from the surface of the ground, and a narrow, gently sloping passage led 200 mm to the surface. Retreat burrows of *C. namaquensis* were usually located in some sort of a redoubt, as clumped vegetation, where the binding roots gave the soil greater cohesiveness, eliminating the danger of cave-ins. Those inhabiting rocky areas either used crevices and fissures in the rocks, or dug burrows in the gravel between rocks. Terentiev (1961) records fossorial habits of Saharan *Chamaeleon vulgaris* (= *Chamaeleo chamaeleon*). Similar burrows are dug by the European lacertid *Lacerta vivipara* (Burrage 1961), and by the American iguanid *Uta stansburiana hesperis* (Burrage 1966).

Camouflage value through colour lability in chamaeleons is synergistic with thermoregulation only at certain temperatures (see pp. 56-7, 59-60). Colour change in chamaeleons is primarily not for concealment, since when annoyed they become black, irrespective of background, and quite conspicuous. Thus, some colour lability in chamaeleons is emotional as the 'excitement pattern' of *Chamaeleo namaquensis* (p. 54). Schmidt & Inger (1965) note a normal *C. ituriensis* is forest green with large, irregular black spots, becoming dark if annoyed, but light green if victorious in combat (Bustard 1965, 1966, 1967c).

Upon the approach of a potential source of harm, *Chamaeleo pumilus* on a twig nearly always turned in an attempt to put the twig between itself and the object of its fear. The value of this is questionable, as in turning it flashes the longitudinally striped ventrum, which directs attention to its movement. Those that remained still were more difficult to detect. If annoyed, or faced with the further threat of harm, they frequently dropped and fell, as is described for *C. dilepis* (Brain 1961), or attempted escape in flight, without the wavering gait. *C. pumilus* did not feign death, as recorded for *C. dilepis* by Brain (1961).

C. namaquensis attempted escape in evasive flight, and could run very fast. However, if chanced upon when at rest, it kept perfectly still, except for the eyes, which rivet on its tormentor. There was no colour change, nor any reaction to having hands passed over them, or fingers straddling them. However, even if lightly touched, especially in the inguinal region, *C. namaquensis* exploded into challenge and fury. Leaping to a high, stiff-legged stance, it quickly became black, and inflated and laterally compressed the body. The throat was gorged, showing the yellow, reddish-orange interstitial skin, and the mouth held widely agape, accompanied to hissing (sounds like 'bissss'), and it often emitted a guttural growl (sounds like 'rrrr'). The mouth of adults has a

yellow-orange interior, while that of the young is black. In this display, *C. namaquensis* turned and faced and frequently rushed its tormentor if further annoyed. Such action was usually quite startling and, in a moment of hesitation on the part of its antagonist, the chamaeleon changed to a lighter pattern and attempted to escape. It was most vicious when trapped, making repeated charges, and snapping its powerful jaws. While *C. pumilus* would bite if held, it was not painful, but a large *C. namaquensis* could inflict a powerful bite. *C. namaquensis* did not release its hold, but biting down hard, twisted and turned, and pushed and pulled in a most vicious manner.

3. *Learning ability*

Detailed studies of learning in reptiles are lacking, but some observations are warranted of evidence of learned behaviour, and modification of instinctive behavioural patterns in the light of past experience of the subject. *Lacerta agilis* (Rollinat 1934), *L. muralis* (Cooper 1958) and the iguanid *Uta stansburiana hesperis* (Burrage 1966) have been shown to demonstrate a Pavlovian response. Furthermore, when prey is in hiding, they attempt to flush it from cover by appropriate means.

Chamaeleo namaquensis and *C. pumilus* did not respond to Pavlovian sound stimuli, but would associate objects with food, as do the previously mentioned lizards. *C. namaquensis* would drink from the nozzle of a plastic squeeze bottle. During a food shortage several small males would accept dead food items such as large grasshoppers trimmed to size, and even devoured pieces of liver or meat. *C. pumilus* learnt to accept food from fingers, and both species quickly came regularly to food dishes, whether they contained a meal or not. Several *C. pumilus* often walked over to the enclosure containing the *C. namaquensis* to take the food of the larger species, successfully bluffing any which challenged them.

In hunting prey older chamaeleons demonstrated techniques which would be modified through experience and continually reinforced. Such instances were: (1) the safe overpowering of prey items capable of harming the chamaeleon; (2) the capture of prey which secretes itself during pursuit. The latter behavioural pattern was evidenced only by *Chamaeleo namaquensis* (see also food habits, p. 75). The chamaeleon would stop at the end of the prey's tracks and begin a careful search of the cover, beating small plants with its feet, or overturning small pebbles and other objects to flush the prey. If prey sought shelter in vegetation too large for the chamaeleon to trample, they lay in ambush until the potential meal emerged of its own accord within a reasonable period. Hatchlings would not do this, and by successive trials (15-25, $\bar{x} = 17$) of securing hidden prey, whether chased or not, the young *C. namaquensis* gradually seems to learn that out of sight prey was under cover.

Chamaeleo namaquensis and *C. pumilus* adults quickly recognized the potential harm that might be inflicted on them by such prey as large spiders, scorpions, hymenopterans, vipers and large lizards. Experienced saurian hunters disabled

the capacity of such prey to inflict harm and seemed to know and recognized which part of the prey inflicted injury. In attacking such prey they adopted totally different tactics. First, they carefully viewed the prey, and then secured it so as to bring the teeth into play at once on that structure capable of causing harm, rather than a general, indiscriminate crushing. They then spat out the prey, viewed it again carefully and repeated the process until they were apparently 'satisfied' that no further danger existed. The prey was then taken in the normal manner. In the case of a large spider they aimed for the chelicerae; a scorpion, its terminal, poisonous sting; a wasp or bee, the most posterior part of its abdomen; a venomous snake or large lizard, its head. In the case of a very large scorpion, they disabled the large, clawed pedipalps after removing the sting. New-born young and hatchlings would not do this, and carelessly grabbed such items, often receiving a painful injury. They then wiped their head on the substrate and tried again. Within three days, all young handled such dangerous prey items as the adults.

The green anole (*Anolis carolinensis*) and another iguanid, *Uta stansburiana hesperis* also behaved similarly (Burrage 1966); seasoned hunters of both species being most cautious in attacking and disabling black widow spiders (*Latrodectes*), as though they fully realize the danger of this arachnid.

H. Food habits

1. Feeding

Chamaeleo pumilus stations itself on shrubs, grasses, reeds and wire fences in situations apt to be frequented by its prey, which it captures mostly by ambush. *C. namaquensis* regularly hunts, patrolling its territories, and securing any suitable prey chanced upon. The tongue only is used by *C. pumilus* and most often by *C. namaquensis* in catching prey. However, *C. namaquensis* often chased small lizards, beetles, and others attempting to escape it. *C. namaquensis* pursued those prey attempting escape, and when overtaking such prey on a parallel course, the chamaeleons simply snapped up the victim in their jaws in the normal saurian manner. They also lay in wait under plant cover and caught any suitable animal walking by, or beat and harried cover into which prey had sought refuge. Both species, but particularly *C. namaquensis*, meticulously masticate their prey before swallowing it, the tongue assisting. One forefoot was sometimes used to manipulate especially large prey.

Burrage (1966) reports that captive *Uta stansburiana hesperis* developed a taste for an egg mixture that was fed to alleviate insect shortages and served as a vehicle for medicine and nutriment for sickly specimens. Sick chamaeleons did not take to such fare and had to be force-fed.

Hotton (1955) gives an interesting and detailed account of the dentition of certain American iguanids, noting that lizard dentition is a reflection of the character of the integument and activity of the prey. In *Chamaeleo pumilus* there are usually 14 teeth in each half of the lower jaw, of which the first two teeth are the smallest, and teeth 6, 7, 11 and 12 are the largest. The teeth are all

even and not tilted. The posterior teeth are broad-based, whereas the anterior teeth are conical. These teeth have faint anterior and posterior crenulations and the last teeth in the row have the central cusp pointing slightly backwards. Teeth 9-14 are set at an angle so that their bases are straight, but oblique to the jaw. There are usually 15 teeth in each half of the upper jaw, of which teeth 12-14 are the largest and tricuspid. The first three teeth are the smallest and conical. The posterior teeth have the main cusp tilted backwards very slightly. Only teeth 12-15 have slight anterior and posterior crenulations. Teeth 4-10 are very broad-based. In occlusion lower and upper jaw intermesh with each other.

In *C. namaquensis* there are usually 15 teeth in each half of the lower jaw, of which the first and fifth teeth are the smallest; teeth 6-10 and 15 are equisized; and teeth 11-14 are the largest. A line drawn through the crown apices is even in the anterior half of the jaw only, since the teeth of the posterior half tilt labially. Viewed from the side, the upper jaw is curved down at mid-point, so that the first and last teeth are at the same level, whereas those in between describe a gentle arc of 80°; the base of the tooth at mid-arc being equal in lateral line to the crowns of the first and last teeth in the jaw. In each half of the upper jaw, there are usually 16 teeth, of which teeth 12-15 are the largest, and from that point forwards they become progressively smaller. The first five teeth of the lower jaw are somewhat conical, especially those most anterior, but all the remaining teeth of both jaws are noticeably laterally compressed and crenulated on their anterior and posterior cutting edges. These crenulations do not show in labial view, because the teeth are slightly convex. The posterior margin of each tooth is somewhat steeper than the anterior margin, and the large central cusp is usually slightly recurved. There are no tricuspid teeth. The upper jaw occludes outside of the lower jaw.

The conical fore teeth in the jaws of both species of chamaeleons hold and prevent escape of the prey. The prey of *Chamaeleo pumilus* falls into all of Hotton's (1955) prey categories of 'low, intermediate, and high activity, and those of light, intermediate, and heavy integument—based on effect of teeth on the integument'. Probably because of its catholic diet, the dentition of *Chamaeleo pumilus* is too complex to fit Hotton's system. In *C. namaquensis* the meticulous chewing shears prey items into neat particles. *C. namaquensis* prey fall into Hotton's (1955) 'heavy integument . . . intermediate activity' prey category. *C. namaquensis* dentition seems most similar to Hotton's Group 'A' dentition, but this is the dentition type of such herbivorous iguanids as *Ctenosaura*, *Dipsosaurus*, and *Sauromalus*. The *Chamaeleo namaquensis* prey would seem to require Hotton's Groups 'D' and 'E' dentitions, but 'D' has little or no lateral compression of the crowns, and neither does 'E' fit, since such teeth are slender and cylindrical. Hotton's other dentition groups do not readily accommodate the teeth of *C. namaquensis*.

Chamaeleon teeth occupy a shallow dental groove in the jaw. Edmund's (1969) description of the number of teeth in *Chamaeleo pumilus* agrees with this

study. Chamaeleons have only acrodont dentition, with teeth added only at the most posterior end of the jaw. Chamaeleons lack any anterior pleurodont teeth as in contrast to the agamids, which also have acrodont teeth. Chamaeleonids and agamids do not show the polyphyodonty of other lizards. The teeth of chamaeleonids and agamids apparently wear down with age, until the jaw margin itself is utilized as a cutting edge, but this was never observed.

Sight is the principal sense of chamaeleons, which aim their eyes (see pp. 71-2) on their prey before securing it. Projection of the chamaeleon tongue is a source of dispute between Gnanamuthu (1930) and Zoond (1933). The former thinks projection of the tongue is due mostly to relaxation of the highly contracted hyoglossi. However, by physiological experiments and anatomical investigation of the muscles and vascular supply of the tongue, Zoond (1933) showed that protrusion of the tongue is effected by the contraction of the geniohyoids, the tongue is held protruded by extreme contraction of the hyoglossi, and that several other muscles and tendinous tubes are important in the final thrust and holding of the target. Retraction is by the interplay of the hyoglossi and the sternohyoids. Zoond showed that several points of Gnanamuthu's surmised chamaeleon tongue action are not supported by physiological or anatomical data.

In some *Chamaeleo pumilus* the tongue pulling power approximated two-thirds of the animal's body weight, but most had a tongue pulling power about 50% of their body weight. *C. pumilus* shot its tongue to a maximum range, roughly equivalent to two-thirds of its total length, exceeding the maximal range observed by Von Frisch (1962). In *C. namaquensis* the tongue has a pulling power equivalent to the body weight of the chamaeleon, and was maximally projected to a distance approximating its snout-vent length. Data are limited on the range and pulling power of the tongue of chamaeleons. Dischner (1958) says a Camerounian *C. montium* weighing 100 g has a tongue pulling power of 43 g. As Dischner (1958) observes, there is no evidence of any adhesive substance on the tip of the tongue, other than the 'normal' adhering quality of a moist object. Pulling the tongue from the mouth of an anaesthetized chamaeleon and placing it on a beetle showed no stickiness, neither was it sticky to the touch. The tongue only held an object to which it was forcibly applied, as would be the case in normal projection. The prey is grabbed and held by a mechanical overlapping of the bi-lobed tongue knob (Fig. 8). What is brought in by the tongue was considered food and eaten, even if the missed edible prey was still in view to a chamaeleon chewing a physical surrogate.

2. Amount of one meal

Chamaeleo pumilus and *C. namaquensis* in the field were voracious feeders, often eating to stomach capacity, and as soon as the preceding meal passed to the small intestine, a new meal was ingested. Size and specificity in prey selection were important in actual meal volume. Table 18 shows the normal volumetric

daily food intake of *C. pumilus* (± 70 mm, s-v) and *C. namaquensis* (± 105 mm, s-v). By selecting tenebrionids and the smaller orthopterans, *C. namaquensis* realized a greater real intake of food than by taking individually larger prey. While the same was true for *C. pumilus*, the wider tastes of this species made it more difficult for this type of analysis. The largest prey taken by *C. pumilus* adults were tettigoniid orthopterans and large vespids, of which two were capacity. Both of these prey items were Food Index '3' at 2 ml volume each. The smallest prey taken by adult *C. pumilus* were fruit flies (Drosophilidae).

Table 18

Volumetric daily food intake of *Chamaeleo namaquensis*¹ and *C. pumilus*².

Example	Prey Food Index	Vol. (ml) each	Number per meal	Daily volume (in ml) per number (in parentheses) of daily meals		
				min.	\bar{x}	max.
¹ Large locustid	5,0	4,5	4	(3) 72,0	(6) 108,0	(8) 144,0
¹ Small locustid	4,0	2,0	30	(3) 180,0	(6) 360,0	(8) 480,0
¹ Large tenebrionid	3,8	1,25	19	(5) 118,75	(12) 285,0	(15) 356,25
" "	3,8	1,25	23	(5) 143,75	(12) 345,0	(15) 431,25
¹ Small tenebrionid	3,5	0,85	19	(5) 80,75	(12) 193,8	(15) 242,25
" "	3,5	0,85	23	(5) 97,75	(12) 234,6	(15) 293,25
² Muscid	2,0	0,25	15	(3) 11,25	(5) 18,75	(8) 30,0
² <i>Tenebrio molitor</i>	4,0	2,0	5	(3) 30,0	(5) 50,0	(8) 80,0
" "	4,0	2,0	7	(3) 42,0	(5) 70,0	(8) 112,0
" "	4,0	2,0	10	(3) 60,0	(5) 100,0	(8) 160,0

C. namaquensis and *C. pumilus* began eating soon after emergence—after early morning defecation of the previous late day meal—the former eating prodigiously while drenched in dripping ground fogs, and the latter on frosty winter mornings. Early morning at emergence and late afternoon chamaeleons ate to their stomach capacities. The number of daily meals is given in Table 18. Of 80 *C. namaquensis* stomachs examined, only 2 were empty, and of 150 *C. pumilus* stomachs examined, only 20 were empty.

Wood (1933) and Burrage (1966) studied food amounts ingested by the American iguanid *Uta stansburiana*, noting variation in consumption with the weather, it being greatest at the hottest times of the year. Seasonal variation in food consumption was not particularly noticeable in *C. pumilus* or *C. namaquensis*.

3. Rates of passage

Feeding marked insects to chamaeleons showed that the last meal of the preceding day was passed on emergence the following day, which was the longest time for digestion (± 12 hours). Digestion of the other daily meals was completed in two to five hours, depending on the integument of the prey. Undoubtedly, the short passage rates reflected the high degree of mastication to which the food was subjected, increasing the area for enzymatic action and absorption.

4. Prey items

In *Chamaeleo pumilus* (Table 19) differences in food ingested were seasonal, but appeared to vary with sex. While dipterous families were usually a predominant prey item in both sexes, quite a considerable part of their prey was taken from other insect orders. For example, females ate mostly dipterans (97,2%, mainly muscids) in June, and the least (2%) in October, whereas males ate only dipterans in February, and the least (50%, almost equivalent amounts of syrphids and muscids) in August, with the remaining prey in August almost evenly taken from immature insects (24,5%) and orthopterans (25%). Orthopterous families were predominant in the winter diet of males, whereas the highest intake (23,4%) of orthopterans was in the February diet of females. Essentially as can be seen in Table 19, what was most taken in the diet of one sex for any given month was taken in different amounts by the opposite sex, and the total consumption of each contained different prey elements. Of note was the amount of ground-living carabids taken, which in May accounted for almost a third of the diet of male *C. pumilus*. Greatest ingestion of carabids (22%) by females was in August. *C. pumilus* were found supratidally at Port Nolloth, and The Strand, feeding on small tenebrionids and flies at the former locale, and exclusively on flies at the latter. Injurious insects formed the major portion of the diet of *C. pumilus*, and the large numbers taken rate this little lizard significant in their control.

Table 20 gives the prey taken by coastal *Chamaeleo namaquensis*, and Table 21 that of inland populations. In the former the predominant item was tenebrionid beetles. The lowest amount of tenebrionids in any monthly sample was 60%, and the monthly mean was never below 93,3%. The inland populations of *C. namaquensis* ate larger amounts of other prey items, especially Orthoptera and Lepidoptera. Some prey, such as buprestids and curculionids were seasonally taken, when these were commonest. However, inland *C. namaquensis* also ate predominantly tenebrionids, and the lowest percentage in any monthly sample was 2,5%, and the monthly mean was never below 67%. Plants were ingested regularly, but more so by coastal *C. namaquensis*. In coastal *C. namaquensis* the largest amount of plants in any sample was 29,1%, and the largest mean 2,8%. In inland *C. namaquensis* the largest amount of plants in any sample was 20%, and the largest mean was 1,5%. Certainly some plant ingestion might be incidental with the prey, but this seems scarcely credible in view of the amounts recorded, nor that *Zygophyllum stapfii* was the predominant plant ingested. Only the fleshy parts of these plants were taken in by the chamaeleons. Inorganic matter composed of small stones, gravel, and sand was more frequently ingested by coastal *Chamaeleo namaquensis*, of which the greatest amount in a sample was 30%, and the largest mean was 6,2%. The greatest amount of inorganic matter in an inland sample was 1,1%, and the largest mean was 0,5%. Inorganic matter might be ingested for assisting in internal, physical degradation of food, and/or parasite removal.

The fact that some *C. namaquensis* had eaten larval beetles was interesting,

Table 19

Monthly prey percentage of male and female *Chamaeleo pumilus* at Stellenbosch, Cape Province.

Contents	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Plants	♂♂ —	♂♂ —	♂♂ —	♂♂ —	♂♂ —	♂♂ —	♂♂ —	♂♂ —	♂♂ —	♂♂ —	♂♂ —	♂♂ —
Miscellany*	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified arthropods	—	—	—	—	—	—	—	—	—	—	—	—
Araneae	—	—	—	—	—	—	—	—	—	—	—	—
Immature insects**	—	—	—	—	—	—	—	—	—	—	—	—
Orthoptera	—	—	—	—	—	—	—	—	—	—	—	—
Cicadellidae	—	—	—	—	—	—	—	—	—	—	—	—
Psyllidae	—	—	—	—	—	—	—	—	—	—	—	—
Aphidoidea	—	—	—	—	—	—	—	—	—	—	—	—
Lygaeidae	—	—	—	—	—	—	—	—	—	—	—	—
Ichneumonidae	—	—	—	—	—	—	—	—	—	—	—	—
Vespidae	—	—	—	—	—	—	—	—	—	—	—	—
Apidae	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified Coleoptera	—	—	—	—	—	—	—	—	—	—	—	—
Carabidae	—	—	—	—	—	—	—	—	—	—	—	—
Coccinellidae	—	—	—	—	—	—	—	—	—	—	—	—
Tenebrionidae	—	—	—	—	—	—	—	—	—	—	—	—
Chrysomelidae	—	—	—	—	—	—	—	—	—	—	—	—
Curculionidae	—	—	—	—	—	—	—	—	—	—	—	—
Neuroptera	—	—	—	—	—	—	—	—	—	—	—	—
Syrphidae	—	—	—	—	—	—	—	—	—	—	—	—
Tephritidae	—	—	—	—	—	—	—	—	—	—	—	—
Caliphoridae	—	—	—	—	—	—	—	—	—	—	—	—
Sarcophagidae	—	—	—	—	—	—	—	—	—	—	—	—
Muscidae	—	—	—	—	—	—	—	—	—	—	—	—
Lepidoptera	—	—	—	—	—	—	—	—	—	—	—	—
Stomachs with food examined	5	4	6	3	8	10	5	7	5	7	5	4
Stomachs empty	2	0	0	2	1	0	1	0	1	1	0	0

— = absent * = shed chamaeleon skin ** = eggs, larvae, and pupae.

Table 20

Prey percentage in given months of a coastal population of *Chamaeleo namaquensis*. The percentage range is shown in parentheses, and when one number is shown it indicates the occurrence of an item in one sample only. The monthly mean is the percentage not enclosed in parentheses.

Contents	February	April	June	November
Inorganic	2,60 (0,01-16,0)	0,56 (0,09-10,0)	6,20 (0,10-30,0)	1,84 (0,20-15,0)
Plants	2,80 (0,01-29,1)	T (0,01-0,2)	0,06 (0,01-1,2)	0,74 (0,01-10,0)
Miscellany*	0,20 (1,0)	T (0,2)	0,02 (0,01-0,8)	T (0,01-0,5)
Unidentified (chiefly arthropods)	T (0,01)	0,01 (0,10-0,3)	0,11 (0,09-4,0)	0,01 (0,50)
Solpugida	—	T (0,6)	—	—
Scorpionida	—	0,10 (8,0)	—	—
Orthoptera	—	T (0,2)	0,06 (0,05-4,5)	0,82 (0,82-25,0)
Hymenoptera	—	—	0,06 (2,0)	0,28 (10,0)
Tenebrionidae	94,60 (70,00-100,0)	99,20 (90,00-100,0)	93,30 (70,00-100,0)	96,34 (60,00-100,0)
Leptidoptera	—	—	0,04 (0,05-4,5)	—
Reptilia	—	0,14 (1,00-5,0)	0,08 (10,0)	—
Stomachs examined	10	8	10	11
Scats	20	39	47	32

— = no record.
T = Trace > 0,001.
* = shed chamaeleon skin; various insect orders, mostly Diptera; intertidal arthropods.
N.B. Columns do not quite add up to 100,0% due to trace items and rounding off.

Table 21

Prey percentage in given months of an inland population of *Chamaeleo namaquensis*. The percentage range is shown in parentheses, and when one number is shown it indicates the occurrence of an item in one sample only. The monthly mean is the percentage not enclosed in parentheses.

Contents	February	April	June/August	November
Inorganic	0,01 (0,50)	—	0,18 (0,60-1,1)	0,50 (1,0)
Plants	—	—	1,33 (0,01-20,0)	1,50 (3,0)
Miscellany*	—	0,35 (0,10-3,0)	T (0,10)	—
Unidentified (chiefly arthropods)	—	—	—	—
Orthoptera	20,09 (15,00-32,0)	2,00 (3,00-25,0)	—	10,00 (20,0)
Buprestidae	—	6,25 (25,0)	—	—
Tenebrionidae	79,09 (60,00-95,0)	66,65 (50,00-99,0)	85,16 (2,50-100,0)	88,00 (76,00-100,07
Scarabaeidae	—	6,25 (25,0)	2,73 (38,00-49,0)	—
Curculionidae	—	—	10,25 (24,00-100,0)	—
Lepidoptera	—	18,70 (99,00-100,0)	—	—
Stomachs examined**	7	6	22 (2)	6
Scats	—	10	7	4

— = no record.

T = Trace > 0,001.

* = shed chamaeleon skin; mammal hair; bird feathers; various insect orders.

** = empty stomachs shown in parentheses.

N.B. Columns do not quite add up to 100,0% due to trace items and rounding off.

since these are mainly fossorial and indicated that *C. namaquensis* occasionally dug up food purposely or ate those unearthed by chance in excavation. It is not known whether the bird feathers and mammal hairs in some inland *C. namaquensis* (Table 21) were the remains of meals or accidental ingestion of feathers and hairs taken in with other prey. Since they were small feathers and hairs, it strongly infers purposeful ingestion of small birds and mammals. A chamaeleon captured at Ganab, near the Great Western Escarpment, had eaten only wasps, but this information is not reflected in Table 21. Some coastal dune-dwelling *C. namaquensis* ate significant numbers of other reptiles (Table 20). In January 1970, at Cape Cross, South West Africa, Dr J. Jurgens collected a chamaeleon that had eaten only reptiles, but this information is not reflected in Table 20. Figure 8 shows a *C. namaquensis* catching a gecko. In the field a male *C. namaquensis* 95 mm long snout-vent was seen to capture and kill a *Bitis peringueyi* 200 mm in total length. At low tide and within the spray of heavy surf, strand-dwelling *C. namaquensis* frequently penetrated seawards of the mean high tide limit on to damp sand. These chamaeleons walked amongst the tidal wrack and fed chiefly on flies, intertidal arthropods, tenebrionids, and reptiles. The ingestion of intertidal arthropods would certainly necessitate a salt gland. Unfortunately, the larger numbers of coastal *C. namaquensis* sampled further inland obscures the actual diet of these strand-dwelling chamaeleons as presented in Table 20.

Burrage (1966) notes that the American iguanid *Uta stansburiana hesperis* takes more flying insects later in the day, when the activity of such forms was restricted to plant cover by increasing wind intensity. *Chamaeleo pumilus* was restricted to plant cover only by the most intense winds, and, at such times, took slightly more flying insects; however, most of its prey was of the winged insect orders. Prey selection by *C. namaquensis* was not affected by wind intensity.

There are no detailed accounts of annual prey ingestion for chamaeleons. Most chamaeleons are insectivorous, though *C. oustaleti* of Madagascar eats mice and birds, and *C. dilepis* and *C. melleri* of Africa take birds (Schmidt & Inger 1965).

5. Skin-shedding

Adult *Chamaeleo pumilus* and *C. namaquensis* in the field shed their skins every six weeks, and juveniles every four weeks. Unhealthy chamaeleons took as much as eight weeks between shedding periods, and had difficulty completely sloughing off the old skin. Time interval between sloughing in *C. pumilus* and *C. namaquensis* agrees with Bustard (1963) for *C. chamaeleon*. Shedding was as in *C. dilepis*, as given by Brain (1961). The old skin whitens over the body and limbs prior to shedding. In *C. pumilus* and *C. namaquensis* the old skin splits along the body in a mid-dorsal line and in the neck region and head. By laboured compression, arching of the body, and rubbing against any rough object the skin is loosened and removed. *C. namaquensis* used its hind feet to remove large patches of skin on the back of the body. Both species used their



Fig. 8.

Chamaeleo namaquensis in the act of catching a gecko (*Rhoptropus afer*). Note bi-lobed nature of tip of chamaeleon's tongue, which totally obscures head of victim. Also of interest, this chamaeleon shows Hoesch's 'Schreckmuster' (see text). Photo through courtesy of Mr H. Maedler, Swakopmund.

jaws to remove the old skin from their limbs. Isolated pieces of skin often persisted along the cranial ornamentations for some time. *C. namaquensis* shed its skin almost in one piece, which it then devoured. *C. pumilus* did a more patchy job of sloughing and was less likely to eat the cast skin.

Further aspects of skin-shedding in reptiles are discussed in the following section.

I. Water and salt balance

1. Drinking and water sources

Chamaeleo pumilus uses its tongue to lap up water drops on plants, but in rains, condensing fog, or drizzle, water drops beading-up on the snout tip were simply run on to the slightly protruded tongue. Occasionally, captives on one twig used the tongue to shoot off water droplets on adjacent leaves. Except during summer, water was readily available to *C. pumilus* in varied forms. In summer, precipitation is less frequent, and at this time dew is the principal source of water. *C. pumilus* always drank early in the day. On rainy days drinking was *ad lib.* through the day, but in clear weather, the early morning drink of dew had to suffice (see water storage and conservation, p. 86).

The water sources available to *C. namaquensis* are the same as that of *C. pumilus*, but the former species rarely encounters rain. Coastal *C. namaquensis* relies mainly on the frequent fogs. On wholly foggy days *C. namaquensis* drinks *ad lib.*, but on clear days fog and dew frequently recurred in the late afternoon and evening when the chamaeleons were still abroad. Thus, on clear days the desert chamaeleon can drink at times early in the day at emergence and late the same day prior to retirement.

C. namaquensis uses its tongue to lap up dew, as well as fog water condensed on vegetation, sand and rocks. It also used the tongue to shoot water drops off adjacent plants. Early in the morning in sparsely vegetated areas, *C. namaquensis* drank from the water-saturated sand arising from condensate run-off from its body. *C. namaquensis* has a fine-grained squamation which serves as fine, very distinct capillary channels leading to the mouth. These channels are especially distinct on the throat and fore-part of the body. If dyed water was placed on the mid-laterum of the body, water moved by capillarity up to the vertebral region, and towards the head and tail. The chamaeleon turned its head to drink the water accumulated on its flanks and vertebral knobs, and in captivity would do so off each other's bodies. Thus, the animal is designed as a 'water collection' surface itself.

Tenebrionid beetles are the principal prey of *C. namaquensis*, and they undoubtedly contribute to the water economy of the chamaeleon. Early in the morning various tenebrionid beetles could be seen upended, with the head buried in the sand and fog water condensing on their thorax and abdomen. The water trickled down to the sand which became thoroughly saturated. Careful removal of the sand around the head showed it to be buried in this water-saturated sand and the jaws working in drinking.

Lizards in areas of moderately high, or regular rainfall, have little difficulty in meeting their water requirements. Most lizards drink essentially as do chamaeleons, but varanids, large iguanids, the larger anguids, teiids and scincids immerse the snout in water to drink. *Chamaeleo pumilus* and *C. namaquensis*, co-inhabitant populations in the Namib Desert at Lüderitz and Port Nolloth, utilize the same water sources. An introduced population of *C. pumilus* at a residence in Walvis Bay had no apparent water-source problem. *C.*

chamaeleon of the Sahara and Levant is the only other chamaeleon of deserticulous habits, but no references to its ecological adaptations have been found. Mayhew (1968) has adequately reviewed water problems of desert lizards. Desert lizards acquire water from: (1) drinking; (2) free water in the food; (3) oxidation water (Schmidt-Nielsen 1964). The helodermatid *Heloderma suspectum* (Bogert & Martin del Campo 1956) needs surface water, and the iguanid *Dipsosaurus dorsalis* and the agamid *Amphibolurus pictus* (Mayhew 1963) copiously drink water if available. *Chamaeleo namaquensis* and *C. pumilus* were both active at times of dew, thus this was a realized water source for them. Since dew occurs on cold nights, most reptiles are considered unable to use this source because they would be inactive (Schmidt-Nielsen & Dawson 1964). However, many desert lizards merely emerge the head, on which the dew may condense and be licked off. The agamid *Moloch horridus* (Davey 1923; Hosking 1923), and iguanids *Phrynosoma modestum*, *P. cornutum*, and *Holbrookia maculata* (Meyer 1966) lick water from plants. Louw & Holm (1972) show the coastal Namib Desert lacertid *Aporosaura anchietae* uses not only condensed fog water directly, but also that condensed on kelp flies.

The hygroscopic skin of the agamids *Cordylus giganteus* (Mertens 1960), *Uromastix hardwickii* (Seshardi 1957) and *Moloch horridus* (Davey 1923) is considered to absorb water by capillary action. Bentley & Blumer (1962) demonstrated that *M. horridus* does not absorb water through the skin, but that the water penetrates fine capillary channels, in which it moves to the mouth and is taken in. Certainly impervious skin would be an advantage to desert forms, and Tercafs (1963) showed variability in dermal permeability of the agamid *Uromastix acanthinurus*, it being permeable when saturated with water, but not in dry air. Warburg (1966) and Maderson (1965a) found that the epidermis of some lizards is water permeable. The iguanids *Phrynosoma modestum* (Weese 1917) and *P. m'calli* (Mayhew 1965) have never been observed to drink in the field or in captivity.

2. Water storage and conservation

The large urinary bladder was flaccid and empty in all *Chamaeleo pumilus* caught in the late afternoon during dry, summer weather. But *C. pumilus* taken earlier the same day after drinking dew had their urinary bladders distended with fluid (Fig. 9). This observation was also true for those taken on rainy days. These field observations were duplicated in the laboratory and are reported later. It seems that since *C. pumilus* always had access to dew, daily water storage was sufficient to get them through the day during dry, summer weather.

C. namaquensis stores a little water in its digestive tract, though the gut is not visibly distended. The gut was also usually crammed with food, so available space for water storage was limited. The urinary bladder of *C. namaquensis* is surprisingly small (Fig. 10A, B), thick-walled with little expansive qualities, and of negligible use for water storage. Unless *C. namaquensis* uses the vascular space



Fig. 9.

Distended urinary bladder of *Chamaeleo pumilus* early on a summer day after drinking dew. Bladder lies approximately between '4' and '5' on mm rule.

for water storage, there seems to be no other visibly apparent water depots. Thus we have the phenomenon of the desert chamaeleon with far less ability to store water than the mesic *C. pumilus*. Coastal *C. namaquensis* apparently obtains sufficient water from the frequent fogs and its food to meet its water requirements. Outside of the fog belt, cloacal reabsorption in conjunction with the salt gland, also allows water economy, and the prey serves as a water source.

Chamaeleo pumilus and *C. namaquensis* excrete a closely packed faeces, which when crushed appeared pasty with hard fragments. The uric acid pellet is excreted first, but attached to the faeces. In these chamaeleons, a water and uric acid mixture can be seen in the ureters. Therefore, it would seem that cloacal reabsorption of water is efficient in both species.

Mayhew (1968) discusses water storage in tissues of desert lizards. Norris & Dawson (1964) found the iguanids *Sauromalus hispidus*, *S. obesus*, and *S. varius* have lateral accessory lymph spaces which are distended with fluid in rainy times and that these storage depots are larger in those forms from more arid regions. The Namib Desert lacertid *Aporosaura anchietae* drinks water copiously and stores it in the digestive tract and vascular space (Louw & Holm 1972). Khalil & Abdel-Messieh (1954) consider the tissues of desert reptiles to have a higher water content than those of mammals, which is disputed by Sokolov (1966).

The gekkonid *Hemidactylus flaviviridis* (Seshardi 1956), agamid *Uromastix*

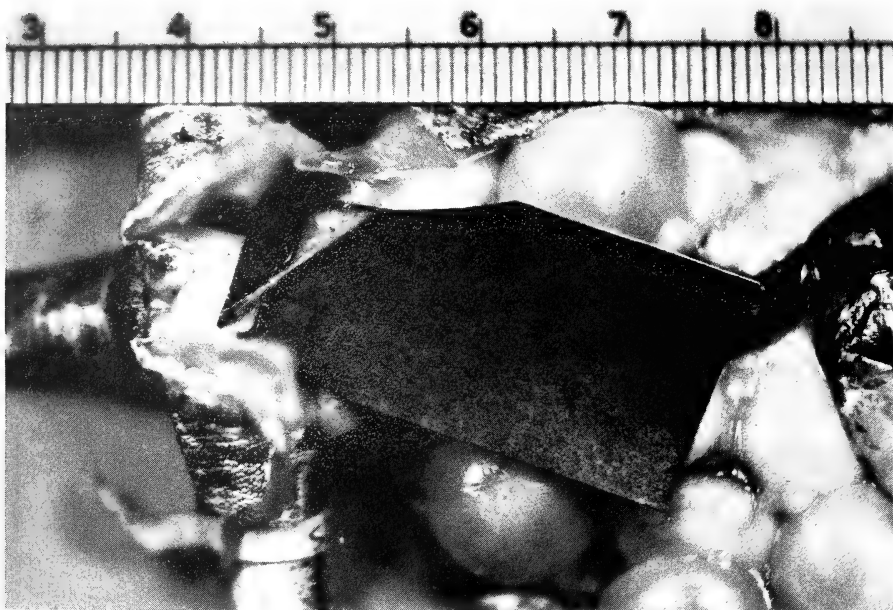
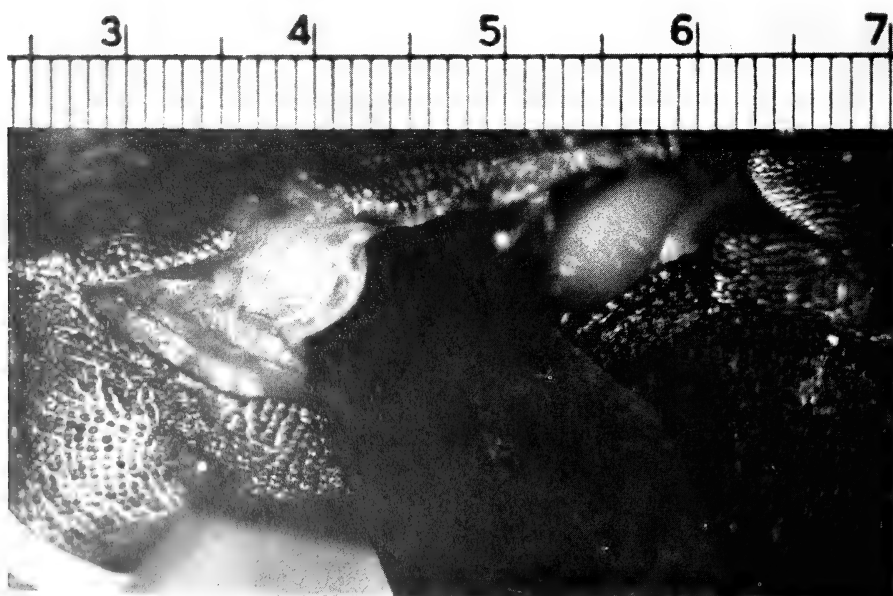


Fig. 10.

A. Flaccid urinary bladder of *Chamaeleo namaquensis*.B. Distended urinary bladder. In both cases bladder lies directly on top of piece of black paper.
Scale in mm.

hardwickii (Seshardi 1957), varanids *Veranus monitor* (Seshardi 1959), *V. gouldii* (Braysher & Green 1970), and scincids *Scincus scincus* and *Chalcides ocellatus* (Khalil 1951) reabsorb water from the urine in the cloaca, excreting the waste as a solid pellet.

3. Water loss

Chamaeleo namaquensis was abroad throughout the day, retiring to its retreat only at night. *C. pumilus* is problematical since it occurs in mesic areas, where desiccation is less extreme, but also in arid areas. *C. pumilus* and *C. namaquensis* pant, which is discussed in the section on thermoregulation (see p. 45). Water loss of chamaeleons in laboratory desiccation studies is dealt with in the next section.

Desert reptiles reduce evaporative water loss by avoiding excessively high temperatures, thus diminishing the use of water in temperature regulation (Schmidt-Nielsen 1963). However, Schmidt-Nielsen (1964) noted little evidence that panting involves a great use of water in thermoregulation even at near lethal body temperatures. The rate of water loss in reptiles is slow (Bentley 1959; Warburg 1965*a, b*) and is exceeded ten times by that of deserticolous rodents (Chew & Dammann 1961). Some desert lizards utilize the higher humidity and lower temperatures in their burrows during extreme midday conditions (Schmidt-Nielsen & Dawson 1964) as do small desert mammals (Schmidt-Nielsen & Schmidt-Nielsen 1950). Evaporative cooling through the respiratory tract enables reptiles a degree of remaining cooler than their surroundings on hot days (Dawson 1967; Dawson, Shoemaker & Licht 1966) and to dissipate 1.3 times the metabolic heat produced at 44 °C in the iguanids *Dipsosaurus dorsalis* (Templeton 1960) and *Crotaphytus collaris* (Dawson & Templeton 1963). At elevated body temperatures oxygen consumption rises and respiration rate increases. As panting ensues, breathing is rapid and monophasic, though oxygen consumption decreases at higher temperatures (Dawson & Templeton 1963; Templeton & Dawson 1963; Dill, Edwards, Bock & Talbott 1935). Consulting Table 16 indicates these relationships to be true for *Chamaeleo namaquensis* and *C. pumilus*, particularly the former.

Benedict (1932), Templeton (1960), and Dawson & Templeton (1963) found evaporative water loss is in excess of water produced, so lizards are dependent on preformed water from their food for maintaining water balance. Since lizards are uricotelic, they gain more oxidation water from protein degradation than ureotelic forms (Schmidt-Nielsen 1964; Schmidt-Nielsen & Dawson 1964). Thus, carnivorous saurians gain considerable water from their prey. Reptiles cannot form hypertonic urine. Roberts & Schmidt-Nielsen (1966) found the kidneys of the iguanids *Phrynosoma cornutum* and *Tropidurus* produce isoosmotic urine, reabsorbing 55% of the glomerular filtrate. Chew (1961) and Bradshaw & Shoemaker (1967) found dehydrated lizards may excrete little urine, but their blood tolerates a greater sodium increase, resulting from electrolyte retention. Shoemaker, Licht & Dawson (1966, 1967) and Dawson

(1967) found the scincid *Tiliqua rugosa*, the gekkonid *Phyllurus milii*, and the agamid *Amphibolurus barbatus* excrete water loads with the least loss of sodium near their particular thermal preferenda. Maderson (1965*b*) hypothesized that skin-sloughing may enable lizards to excrete wastes without losing water.

Chew (1961) and Chew & Damman (1961) considered the skin of some reptiles to be nearly waterproof. However, cutaneous water loss recently has been shown to be a significant avenue of loss, often exceeding that lost via respiration and excretion. Of several reptiles from habitats of varying degrees of aridity, *Sauromalus* (most arid) lost the least (5% of *Caiman*). Cutaneous evaporation in *Sauromalus*, however, was the chief avenue of loss, accounting for 66% of the total water loss at 23 C. Other examples of cutaneous evaporative loss as a percentage of the total water loss are: the arid-dwelling iguanid *Uta stansburiana* 39% and the more humid iguanid *Anolis* 42%—at 30 C (Claussen 1967), at 30 C, 57% in the gekkonid *Gehyra variegata*, and 59% in the agamid *Amphibolurus ornatus*, and at 20 C, 70% in both of the preceding forms (Dawson *et al.* 1966). Maderson (1964) feels the main site of cutaneous water loss in reptiles is the hinge area around the scales. Temperature controlled water loss is that via respiration, and the humidity affects the rate of cutaneous water loss (Warburg 1966).

4. Laboratory desiccation studies on *Chamaeleo pumilus* and *C. namaquensis*

Table 22 shows the body weight losses of the chamaeleons without food or water for seven days and Table 23 gives the haematocrits and plasma osmolality values (with the significance at 'P' level) of the de- and rehydrated groups of this experimental set of *Chamaeleo pumilus* and *C. namaquensis*. Significant differences in the haematocrit are shown between dehydrated *C. pumilus* and dehydrated *C. namaquensis*; between dehydrated *C. pumilus* and *C. namaquensis* and those rehydrated. There is no significant difference between

Table 22

Weight changes (in grams) of ten *Chamaeleo pumilus* and ten *C. namaquensis* desiccated for seven days, giving body weights at the start and the conclusion of dehydration, body weight losses during dehydration, and body weight changes after rehydration. Means are shown in parentheses.

	In	Dehydrated body weights Out	% loss	Rehydrated body weights at death
Dehydrated				
<i>C. pumilus</i>	8,0-12,4 (10,3)	6,2-10,8 (8,5)	16,8-29,0 (21,7)	
<i>C. namaquensis</i>	17,8-82,3 (55,5)	15,8-77,0 (52,0)	4,6-12,4 (7,1)	
Rehydrated				
<i>C. pumilus</i>	6,4- 9,5 (8,4)	5,3- 7,9 (7,0)	13,1-22,6 (16,7)	6,2-10,2 (8,7)
<i>C. namaquensis</i>	49,7-90,1 (60,7)	45,9-84,9 (56,2)	2,3-12,3 (7,6)	47,2-88,0 (57,8)

rehydrated *C. pumilus* and *C. namaquensis*. In plasma osmolality values there is a significant difference between dehydrated *C. pumilus* and dehydrated *C. namaquensis*, and between dehydrated and rehydrated *C. pumilus*, but no significant difference between rehydrated *C. pumilus* and *C. namaquensis*, nor between dehydrated and rehydrated *C. namaquensis*. These data suggest a degree of water storage in the vascular space of both chamaeleons.

Table 23

Haematocrits, and plasma osmolalities, with relevant statistics for ten *Chamaeleo pumilus* (Cp) and ten *C. namaquensis* (Cn) subjected to seven days' desiccation at 0% humidity. At day seven, the rehydrated half of each group were killed and the remainder then rehydrated and killed the following day.

	Haematocrits	Dehydrated	Rehydrated
Dehydrated			
Cp . . .	28.6-33.7 (\bar{x} = 31.3; S.D., 2.4)	Cn ^a P = <0.001	
Cn . . .	14.6-19.8 (\bar{x} = 17.6; S.D., 2.3)		
Rehydrated			
Cp . . .	14.5-29.0 (\bar{x} = 21.4; S.D., 6.0)	Cp ^{a, b} P = >0.2	Cn ^{a, b} P = >0.2
Cn . . .	15.5-32.5 (\bar{x} = 24.6; S.D., 7.4)	Cn ^{a, b} P = >0.2	
Dehydrated			
Cp . . .	395-440 (\bar{x} = 421.3; S.D., 19.0)	Cn ^{a, b} P = >0.2	
Cn . . .	230-255 (\bar{x} = 246.3; S.D., 11.1)		
Rehydrated			
Cp . . .	200-210 (\bar{x} = 203.8; S.D., 4.8)	Cp ^a P = <0.05	Cn ^{a, b} P = >0.2
Cn . . .	219-292 (\bar{x} = 261.3; S.D., 35.4)	Cn ^{a, b} P = >0.2	

The results of the experiment on the survival of *C. pumilus* and *C. namaquensis* with food but no water for twelve days and food and water for an additional three days are given in Tables 24 and 25. Due to the difficulty in acquiring sufficient numbers of *C. namaquensis* in respect of all the studies conducted, the numbers here are too small for statistical analysis. The striking feature is the mortality of half of the *C. pumilus* by the sixth day and the badly dehydrated state of the survivors at the end of the dehydration period. The two taken for an additional three days with water quickly recovered some of their weight loss. Even the deserticolous *C. namaquensis* showed some dehydration and had one mortality, from unknown causes, during the experiment. All of the rehydrated *C. namaquensis* showed an increase in body weight on the first day of rehydration, but at sacrifice had lost more than they had gained, despite having food and water. Both species ate less without water, and easy faecal elimination seemed hindered. The haematocrit and plasma osmolality values of the dehydrated and rehydrated chamaeleons in this experiment approximated those given for the chamaeleons in the preceding experiment.

Upon rehydration in both experiments *C. pumilus* strained and ran to the water, drinking so fast that it choked, and regurgitated, but kept drinking until satiated. *C. namaquensis* acted likewise, but it also chewed water-saturated vegetation, which it spat out, and rolled, ploughed, and rubbed its body in wet sand. Upon sacrifice, both sets of rehydrated chamaeleons contained

considerable ingested water, especially evident in the urinary bladder of *C. pumilus*, and the digestive tract and urinary bladder of *C. namaquensis*.

Freshly caught *C. pumilus* (elev. 105 m) had a haematocrit of 29.0–30.5 ($N = 7$; $\bar{x} = 29.9$; S.D.; 0.63), and plasma osmolality values of 200–210 ($N = 8$; $\bar{x} = 203.8$; S.D.; 5.23). Freshly caught *C. namaquensis* had haematocrits of (coastal; elev. 12 m) 42.0–49.0 ($N = 10$; $\bar{x} = 44.5$; S.D.; 2.28), (inland; elev. 407 m) 46.0–50.0 ($N = 7$; $\bar{x} = 48.7$; S.D.; 1.38), and plasma osmolality values of 220–290 ($N = 8$; $\bar{x} = 259.8$; S.D.; 28.64). The wide range of the S.D. of the plasma osmolality values of *C. namaquensis* may reflect individual differences, the fact that the sample did not separate inland and coastal specimens, or the delay in sacrificing the animals.

Table 24

Body weight losses (in grams) for 3 day periods for 8 *Chamaeleo pumilus* (Cp) and 8 *C. namaquensis* (Cn) for 12 days with food but no water. At the end of 12 days, 2 *C. pumilus* and 6 *C. namaquensis* were given water and food for an additional 3 days (see Table 25). Means are shown in parentheses.

	Days				Body weights		
	1-3	4-6	7-9	10-12	In	Out	% loss
	Body weight losses						
Cp	0.8-1.5 (1.1)	0.6-1.3 (0.9)	0.4-0.8 (0.5)	0.3-0.5 (0.4)	6.1-11.3 (8.7)	3.4-8.6 (6.2)	23.9-44.3 (29.9)
Cn	0.5-4.9 (2.1)	0.4-4.3 (1.5)	0.3-3.2 (1.6)	0.4-1.6 (0.9)	36.0-91.4 (60.8)	31.0-77.4 (54.9)	3.3-15.3 (9.6)

Table 25

Weight changes (in grams) of *Chamaeleo pumilus* (1-2) and *C. namaquensis* (3-7) which were given water and food for 3 additional days after receiving only food for 12 preceding days (see Table 24).

Days 13 to 15

Id. No.	Body weight		Rehydration Maximum body weight (day in parentheses)	3 days Total losses		Remarks
	In	Out		Uric acid	Faeces	
1	12.5	14.0	14.0 (15)	0.12	0.67	
2	8.5	9.2	9.2 (15)	0.06	0.22	
3	50.5	50.3	53.3 (13)	0.16	1.32	
4	48.5	48.8	49.2 (13)	0.28	2.91	
5	49.0	47.5	50.0 (13)	0.31	0.80	shed skin day 13
6	60.3	60.1	62.0 (13)	0.17	1.98	
7	77.4	73.7	79.3 (13)	0.67	3.40	shed skin day 13

Water is obviously crucial to chamaeleons, as was first observed by Brehm (1893), latterly by Bustard (1963), Von Frisch (1962), and experimentally shown in this study. Starving and dehydrated chamaeleons, as those shipped a distance, will drink before they feed, even if food is abundant. They cannot survive on food alone, as the laboratory tests demonstrate. Even humidities of 40–50% experienced by the animals given food and no water

did not assuage them, yet this humidity was experienced by them in the field, and actually a trifle low for coastal *C. namaquensis*.

Minnich (1970) estimates that *Dipsosaurus dorsalis* loses via defecation 61% of its total water intake, and water loss studies under simulated natural conditions apparently show that this iguanid cannot balance evaporative water loss through oxidative water production at the low humidities it encounters when active. A loss via defecation of 61% of the total water intake seems a bit high in the light of studies on cutaneous water loss in reptiles. Perhaps *D. dorsalis* has less cutaneous water loss than another desertic iguanid, *Sauromalus*, though it seems doubtful. Comparison of chamaeleons with other reptile desiccatory studies is difficult, since the dehydration period varies. Claussen (1967), for example, kept his animals in the drying chamber for only 24 hours. Furthermore, he was able to collect faecal and uric acid eliminations in a manner not possible in this study. Faeces and uric acid were weighed as promptly as possible, while they were still moist and freshly eliminated. However, such data seem too open to variables and, thus, are not given here.

Louw & Holm (1972) found *Aporosaura anchietae* haematocrits (dehydrated) of 43–48 (\bar{x} = 45); (rehydrated) 41–46 (\bar{x} = 44), and osmolality values (dehydrated) of 410–435 (\bar{x} = 420); (rehydrated) 390–415 (\bar{x} = 406), and 'normal' of 275–320 (\bar{x} = 312). Freshly caught and rehydrated *Chamaeleo pumilus* haematocrit values agree with those (26,0–35,0; \bar{x} = 29,7) given by Thorson (1968) for terrestrial sauria, but those for rehydrated *Aporosaura anchietae* (Louw & Holm 1972) and for this study for normal and rehydrated *C. namaquensis* do not. This may be due to Thorson's use of the tropical, non-arid saurian, the green iguana (*Iguana*); however his values (25,0–34,0; \bar{x} = 29,6) for the deserticulous tortoise (*Gopherus*) are still much lower than those for the desert-dwelling *Aporosaura anchietae* and *Chamaeleo namaquensis*. Thorson notes the similarity in haematocrit values of those reptiles inhabiting the two desiccatory environments of sea and land, and deserts are the most drying.

5. Salt balance

Figure 11A, B shows a close-up of the salt exudate around the nares of a captive juvenile *Chamaeleo namaquensis*. In *C. namaquensis* the salt gradually exudes in the manner of a brine, forming a considerable deposit as it dries, through which runs a small air passage. When the encrustation gets too large, it is rubbed off with the feet or by scraping the nose against some object. Though *C. pumilus* inhabits supratidal bushes and may ingest animals with a high salt content, no evidence of salt excretion was observed for this species. Collected from *C. namaquensis*, the dry salt exudate was dissolved in 0,1 ml of distilled water. The exudate contained 7 mEq/L of potassium; 45 mEq/L of sodium; and 49 mEq/L of chloride. While captive *C. namaquensis* occasionally ingested water-drenched plants, especially succulents, for water, those in the field not infrequently had plant matter (see food habits, p. 79) in their digestive tracts. The finding of potassium in the nasal salt exudate may indicate



Fig. 11A-B.
Close-up views of nasal salt exudate in *Chamaeleo namaquensis*. Note air passage in Fig. 11A.

an ability to utilize desert plants for food as well as water. Either way it is most interesting, since we may have an omnivorous chamaeleon, excreting salts extrarenally as an adaptation to diet and utilization (plant-chewing) for maintaining water balance. Several lizards (Neill 1958; Burrage 1966) prey intertidally on marine arthropods along desert shores, and undoubtedly take in with such prey some quantity of salt which must be eliminated. *C. namaquensis*, inhabiting the Namib Desert littoral, is the only chamaeleon known to exploit this niche.

Schmidt-Nielsen (1963) feels extrarenal salt excretion is related to cloacal water reabsorption. This may be necessary for production of a low water content urine and efficient cloacal water conservation. The cations of sodium and potassium are actively reabsorbed, with water following passively, which method requires far less work than active water transport. The salt gland serves, then, to eliminate excess cations, which would be primarily potassium in herbivorous and sodium in carnivorous forms.

Schmidt-Nielsen (1965) gives a good general physiological and anatomical account of salt glands; Roberts & Schmidt-Nielsen (1966) also describe the structure of the gland. The reptile salt gland is structured as that of other vertebrates, with branching secretory tubules arranged radially around a central duct. Most studies on salt-excreting saurians have been done on herbivorous forms, which excrete primarily potassium. Templeton (1963, 1964) showed the iguanids *Ctenosaura pectinata* and *Sauromalus obesus* excrete 950 mEq/L of potassium at 190 times plasma concentration, being similar to renal tubule secretion in mammals. Potassium predominates even when the animals were injected with sodium chloride. Other salt-excreting saurians are *S. hispidus*, *S. varius* (Norris & Dawson 1964), *Dipsosaurus dorsalis* (Schmidt-Nielsen, Borut, Lee & Crawford 1963; Templeton 1966), agamids *Uromastix aegyptus* (Schmidt-Nielsen *et al.* 1963), *U. acanthinurus* (Grenot 1967), and the non-arid-dwelling tropical iguanid *Iguana iguana* (Schmidt-Nielsen *et al.* 1963) which secretes potassium as a bicarbonate. These lizards are all primarily herbivorous and the salt-excreting gland serves to remove the salt loads, of which potassium is the major cation, derived from the halophytes on which they feed, which cannot be excreted by their kidneys. Norris & Dawson (1964) consider excretion of potassium by the salt gland of *Sauromalus varius* a physiological adaptation of deserticulous herbivorous lizards to utilization of halophytic plants.

J. Population structure

1. Density and biomass

The high survival of adult *Chamaeleo pumilus* (Table 26) and *C. namaquensis* (Table 27) suggests the very young either bore the brunt of predation or were harder to locate. Adult *C. pumilus* were recovered at a higher rate than juveniles, though after two to three months the juvenile recovery rate stabilized, thus indicating a high mortality of the very young. Of 40 juvenile and adult *C. pumilus* marked in February 1969, 40.0% were recovered in February 1971.

Table 26

Number of *Chamaeleo pumilus* adults and juveniles marked each month (vertical column) and subsequently recovered in later months (horizontal column). As juveniles of a given month mature they are included with the adults of that month.

N marked		Mar.		Apr.		May		June		July		Aug.		Sep.		Oct.		Nov.		Dec.		Jan.	
		Ad't	Juv.	Ad't	Juv.	Ad't	Juv.	Ad't	Juv.	Ad't	Juv.	Ad't	Juv.	Ad't	Juv.	Ad't	Juv.	Ad't	Juv.	Ad't	Juv.	Ad't	Juv.
Feb.	20	20	50	65	35	35	30	45	40	40	30	65	40	65	0	90	0	55	0	0	0	55	0
Mar.	25	30	—	—	33	24	0	32	13	36	13	56	33	36	20	68	33	56	0	60	0	33	0
Apr.	17	10	—	—	—	59	60	29	20	29	50	35	50	29	50	41	40	53	30	47	0	29	0
May	15	8	—	—	—	—	—	60	50	60	37	53	37	53	50	47	25	60	32	33	25	47	0
June	20	1	—	—	—	—	—	—	—	40	0	50	0	15	0	55	0	35	0	40	0	40	0
July	9	0	—	—	—	—	—	—	—	—	—	67	0	67	0	44	0	44	0	22	0	44	0
Aug.	13	0	—	—	—	—	—	—	—	—	—	—	—	54	0	38	0	38	0	8	0	0	0
Sep.	15	20	—	—	—	—	—	—	—	—	—	—	—	—	—	53	25	27	20	0	40	33	85
Oct.	53	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	45	0	28	0	26	25
Nov.	2	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dec.	141	25	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Jan.	10	23	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Percentage recovered in

Of 11 coastal juvenile *C. namaquensis* marked in June, overall recovery in November was only 27.2%, of which all were males, for a male recovery of 45.4%. Of the 41 coastal juveniles marked in November, 48.7% were recaptured in February. Of 21 males marked in November, 52.3% were recovered in February. In February, 45.0% of the females were recovered, of the 20 marked in November. Only in February did marked juveniles (53.4%) exceed adults, though since these juveniles were all coastal, they were actually a larger component of this population (58.5%).

Of 207 marked *C. namaquensis* adults, only 17 were not definitely maintaining territories. As the number removed for research purposes is not included, the biomass (mean weight of chameleons per hectare) of *C. namaquensis* (Table 27) and *C. pumilus* (Table 28) could be considered somewhat above what is given.

Table 27

Mean density per hectare, body weight, and biomass (in grams) of juvenile and adult *Chamaeleo namaquensis* based upon a composite of two study stations.

	Monthly total marked (recovered and new)		Mean weight	Mean weight	Per hectare		Percentage of adult recovery marked in		
	Adults	Mean weight	Juveniles		Density	Biomass	April	June	Nov.*
Apr.	45.0	37.5	—	—	0.5	18.8	—	—	—
June	56.0	53.8	11.0	7.0	6.1	70.8	43.2	—	—
Nov.	57.0	56.1	41.0	3.5	21.2	111.0	24.3	40.0	—
Feb.	49.0	65.3	55.0	8.0	23.4	238.8	40.5	36.0	20.8
Mean	51.8	53.1	35.6	6.1	12.8	109.9			

* Months at far left should be read for recovery month of adults. Juvenile recovery is discussed in the text.

Table 28

Mean density per hectare, body weight, and biomass (in grams) of adult and juvenile *Chamaeleo pumilus* based upon a composite of all study stations. (See Table 26 for percentage recovery per month.) N.B. As juveniles of a given month mature they are included with the adults of that month.

	Adults	Mean	Mean	Total	Density	Biomass
		weight	Juveniles	weight		
Feb.	20	13.5	20	1.0	40	290.0
Mar.	35	8.5	42	1.5	77	361.0
April.	43	7.4	34	1.7	107	363.7
May.	38	8.8	20	1.5	58	364.4
June.	51	11.0	16	1.6	67	586.6
July.	48	11.5	18	1.7	66	582.6
Aug.	70	6.5	29	1.8	99	507.2
Sept.	66	10.5	35	0.6	101	714.0
Oct.	120	9.3	35	1.0	155	1 151.0
Nov.	89	9.3	22	0.6	111	846.3
Dec.	195	12.5	39	0.5	234	2 456.0
Jan.	118	9.5	56	0.8	174	1 165.8
Mean	75.2	9.9	29.6	1.3	107.4	802.0

Biomass of *Chamaeleo pumilus* was highest in December, no doubt reflecting the increasing proportion of young and older juveniles. It is not certain whether the slow climb from February to May is best assigned to an increase in marked individuals, a reflection of actual conditions, or both factors. Biomass of *C. namaquensis* was highest in February. But that of adults was relatively consistent; monthly variations merely reflecting increased weights of reproductively active adults, and addition of juveniles. Since juveniles were not territorial and were tolerated in the territories of the adults, biomass of juveniles in a given area often exceeded that of adults.

The density of *C. pumilus* varied with habitat, being densest on reeds surrounding still bodies of water, as vleis, and least in brushy areas. Density in brushy areas never exceeded 12 ($\bar{x} = 8$) per hectare, of which males composed approximately 45% of the population. In reedy areas densities ranged from 75 to 200 ($\bar{x} = 90$) per hectare, of which males were 40–51% ($\bar{x} = 47\%$) of the population. These data are not reflected in the tables. Differences in habitat density for *C. namaquensis* are apparent in Tables 32 and 33, but these data are somewhat misleading, since more time was spent at coastal locales. Also, there is a big difference between 'inland' and 'coastal' dunes. Inland dunes have vegetation-covered hummocks at their bases, which are lacking in coastal dunes which only have very meagre and scattered single grasses, predominantly *Eragrostis spinosa*. Because these inland vegetated hummocks were on true dunes, they were considered to be part of the dunes, whereas coastal vegetation-covered dune hummocks were accumulations of dune sand on flat areas, apart from dunes. Though found throughout the desert, *C. namaquensis* was most numerous in topographically varied areas.

In February juvenile *Chamaeleo pumilus* (Table 29) were at parity with the adults and in March 56% of the population, and least evident (16,8%) in

Table 29

Population structure (in per cent) of 346 adults and 148 young in the marked population of *Chamaeleo pumilus*. Large follicles are those having a diameter of 5 mm or greater.

Month	Females				Males	
	Juveniles	Pregnant	Yolked follicles		Active	Inactive
			Large	Small		
Feb.	50,0	12,5	0,0	20,0	17,5	0,0
Mar.	54,5	15,6	5,2	9,1	15,6	0,0
Apr.	38,5	5,7	27,2	5,7	12,9	10,0
May	34,5	13,8	8,6	8,6	20,7	13,8
June	23,9	17,9	11,9	11,9	4,5	29,9
July	27,3	33,3	10,6	0,0	0,0	28,8
Aug.	30,0	34,0	5,0	4,0	27,0	0,0
Sept.	34,0	23,0	8,0	10,0	22,0	3,0
Oct.	22,6	28,4	6,5	8,3	30,3	3,9
Nov.	19,9	25,2	13,5	6,3	35,1	0,0
Dec.	16,8	16,8	12,8	13,7	39,0	0,9
Jan.	32,3	23,7	3,5	4,2	36,3	0,0

December. *C. pumilus* males were usually slightly in the minority (see also Hogben & Mirvish 1928a, b; Zoond & Eyre 1934), and in some months males were outnumbered by a considerable margin. Only in November were female *C. pumilus* greatly outnumbered by males. Juvenile *C. namaquensis* (Table 30) were predominant in February (58,5% coastal; 53,4% overall) and a significant component in November. Tables 27 and 30 reflect overall, rather than one population data. Male *C. namaquensis* were somewhat more predominant in June and November, almost at parity with the females in August (inland data only), and the minority sex in February and April.

Table 30

Population structure (in per cent) of 207 adults and 107 juveniles in the marked population of *Chamaeleo namaquensis*. Large follicles are those having a diameter of 5 mm or greater.

Month	Females				Males	
	Juveniles	Gravid	Yolked follicles		Active	Inactive
			Large	Small		
Feb.	53,4	2,8	18,2	3,7	21,1	0,8
Apr.	0,0	40,0	0,0	17,8	42,2	0,0
June	14,2	12,9	6,5	24,6	41,5	0,0
Nov.	41,8	9,2	14,3	9,2	19,4	6,1

Over 27 months Bourgat (1968a) marked 140 *Chamaeleo pardalis* on Réunion Island, of which 80 were lost, 54 recovered over several subsequent weeks, and six recovered several months later. Unlike *C. pumilus* and *C. namaquensis*, *C. pardalis* males outnumbered females 6:1, males being most abundant in December to April, but tend to hibernate in cooler times, whereas females are in evidence throughout the year. Bourgat observed 632 males, 382 females, and 31 young. No young were uncovered in January, April to June, and August. There are no other ecological field studies on chamaeleons, and in this respect, statements of chamaeleon population structure are rather premature.

The spatial relationships of American saurians, especially iguanids, have been the most studied, and good reviews are those of Rand (1967), and Mayhew (1968). However, almost all of these are of no comparative value for *Chamaeleo pumilus*, since the iguanids studied are not arboreal, and of doubtful value for *C. namaquensis*. Most studied saurians have an almost 50:50 sex ratio. Population density has been thoroughly investigated in *Uta stansburiana* and related insular forms of *Uta* (Soulé 1964); *U. s. hesperis*, *U. stejnegeri*, and *U. elegans* (Burrage 1966); *U. s. stansburiana*, and *U. stejnegeri* (Tinkle 1961, 1967; Tinkle, McGregor & Dana 1962; Tinkle & Woodard 1967). The average inland density is approximately 25,5 territory-holding adult utas per acre (about 63,6 per hectare), while that of littoral and insular populations is two to three times as dense. Very few tropical species have been studied, but Harris (1964) reports of 36 *Agama agama* per acre (about 90,0 per hectare) with a biomass of about 2 000 grams (about 5 000 g per hectare). According to Cagle (1946), *Hemidactylus*

on Tinian have a density of 500 adults in a 2 400 square feet area (about 223,0 m²), so assuming even distribution this gives 10 000 per acre (about 25 000 per hectare). Larger species have lower densities and all sizes of tropical species the highest. Shore-dwelling and insular populations have higher densities than those inland, even those adjacent to the coast.

Data are meagre on survival of lizard populations and those available indicate widely different demographics in different species populations. Almost all are concerned with temperate iguanids, save the tropical *Basiliscus* and *Anolis*; *Cnemidophorus* (temperate) and *Ameiva* (tropical) are teiids, and *Amphibolurus* is an Australian agamid. Blair (1960), calculating on theoretical natality rather than juveniles actually marked, estimated that 6–20% of hatchling *Sceloporus olivaceus* reached maturity and 20% of the adults survived to a second breeding season. Fitch (1956) reports almost 40% of young *Crotaphytus collaris* reach sexual maturity, about 20% of these surviving a second season. Crenshaw (1955) reports *Sceloporus undulatus* hatchlings suffered a 50% loss during their first six weeks, and 68% in their first two months; a mortality schedule similar to that reported for *Uta stansburiana* by Tinkle (1967). Burrage (1966) observes that the brunt of predation is borne by the very young and adult females in *U. s. hesperis*. Less than 10% of *Basiliscus vittatus* and *Ameiva quadrilineata* live for one year and only 2% of *Basiliscus* survive two years (Hirth 1963). Essentially, annual turnover is suggested in *Anolis limifrons* (Sexton, Heatwole & Meseth 1963) and *Amphibolurus isolepis* (Storr 1965), but these are based on size groupings present at different times of the year, rather than recovery of marked animals. Fitch (1958) records a 50% yearly reduction of adult *Cnemidophorus sexlineatus*.

2. Social interactions

Chamaeleo pumilus defended only its perches and such territorial conflicts were noted in all months at homo- and heterosexual levels. There were more such disputes between females in winter, more between males in summer, though overall territorial disputes were seasonally constant. Table 31 documents

Table 31

Number of social interactions observed in the field in coastal and inland populations of adult *Chamaeleo namaquensis*. (Table is set up to show the defender on the left *versus* the transgressor on the right, hence the two sets of heterosexual combat.)

Month		Social Interactions				Copulation ♂♂ and ♀♀
		♀♀ vs. ♀♀	Territorial conflicts		♂♂ vs. ♀♀	
			♀♀ vs. ♂♂	♂♂ vs. ♂♂		
Feb.	Coast	17	0	12	0	0
	Inland	6	0	2	0	1
Apr.	Coast	51	14	43	10	104
	Inland	0	0	0	0	0
June	Coast	15	1	10	0	5
	Inland	5	1	0	2	7
Nov.	Coast	0	0	3	3	0
	Inland	0	0	0	0	0

C. namaquensis social interactions in the field at various contact levels. The territorial structure of *C. namaquensis* was such that interactions were between neighbouring individuals mainly on the finely delimited borders of their respective territories. They often inflicted considerable damage on each other in such defence. As defenders, females were involved in more homo- and heterosexual territorial defence than males, but were not observed in any in November, and no heterosexual combat in February. Males defended their territories throughout the year, but were not observed to engage in heterosexual disputes in February. Courtship and coition in both species is discussed under courting in the reproduction section (see p. 111).

3. Territorial display

Territorial displaying *Chamaeleo pumilus* gorged the throat, which had orange interstitial skin in Stellenbosch specimens, but purple in those from Port Nolloth. *C. pumilus* laterally compressed the body which assumed Colour Index '5' and facing-off delivered a series of five side-to-side head bobs in a right and left horizontal 'T', starting and finishing on the right. Head bobs 1 and 5 were at the top arm of the right 'T', and head bob 2 at the top of the left 'T'. These bobs were more like flicks, so quickly and precisely were they executed. An entire set was delivered in 1,2 to 1,4 ($\bar{x} = 1,35$ sec) seconds. Four sets constituted a threat series, with 1,5 to 1,7 seconds intervals between each, and 1,9 to 2,2 seconds intervals between each series. Refusal of the transgressor to leave resulted in fight in *C. pumilus* in the field and in several observations vicious attacks resulted when the transgressor refused to acknowledge the defender's display. Frequently, they fell from trees with interlocked jaws. No deaths resulted, as in *C. namaquensis*, but severe injuries were incurred. As with *C. namaquensis*, females were more aggressive than males.

C. namaquensis territorial display consisted of lateral body compression, a stiff-legged erect stance, gorged throat (displaying purple interstitial skin) and partly gaping mouth, either Colour Index '5', excitement pattern (Hoesch's 'schreckmuster'), or in combination. In delivery, the combatants 'faced-off', with much hissing, head-bobbing, and weaving of the whole fore part of the body side-to-side, up and down; the rear was virtually stable, except in especially heated displays. Looking head on, the head-bobbing was laterally in the horizontal plane, describing an 'S' lying on its side, with the first and last bobs being delivered on the right. Five such bobs constituted a set (delivered in 2,8 sec), two to three sets per display with a one second interval between each. Refusal of the transgressor to leave the defender's presence resulted in combat, in which severe, often fatal, injuries were incurred. There was no 'submissive posture'; only flight of the transgressor averted a fight. Two patrolling *C. namaquensis* often displayed from their respective sides of a common border along its entire length.

A discussion of the literature in respect and synthesis of social interactions and display is included with that on territories.

4. Size and structure of territories

Chamaeleo pumilus had an undefended, shifting, vertical home range, with a vigorously defended night-time rest area. Shifting occurred only if the home range did not provide adequate food throughout the year. *C. pumilus* frequently walked considerable distances to locate new food sources. In plan view the home range area was about 10 m² in both sexes, but since it was at several different horizontal levels, or 'multi-storied', the actual area was much more. For example, *C. pumilus* occupying a bush 3 m high and of 10 m² in plan view with 20 such multi-storied plan areas, the actual home range area was about 600 m². It is, therefore, a more effective use of space. Juvenile *C. pumilus* had no sleeping area that they regularly used for a long time, and a continuously shifting home range.

For simplicity territories occurring in various biotopes and habitats have been placed under the type in which a given territory has most of its area. Such territories embracing different biotopes or habitats were considerably larger than most of those that were limited to one. Territory data are summarized in Table 32 and given in detail of biotope and/or habitat in Table 33. Maximum individual territories occurred in November for coastal males (8 000 m²), females (1 632 m²), inland males (1 752 m²), and females (998 m²), but mean territory sizes were largest in April (male; 2 429,0 m²; female; 885,7 m²—coastal only). One would suspect this to be true for inland populations, but insufficient data are available, thus, the maximum mean (1 435,7 m²) of inland male territories was in June, and females (881,8 m²) in November. Territories appeared to vary in size according to reproductive demands, that is, male territories generally increased in area during courting and those of females were enlarged during egg-laying.

Table 32

Summary of seasonal variation in territory sizes (in square metres) in coastal and inland populations of *Chamaeleo namaquensis* in South West Africa. Means are in parentheses. (For a detailed consideration by biotope and habitat, see Table 33.)

	N	Coastal		N	Inland
Feb.					
♂♂ 16		771-6 800 (1 294,8)		4	1 109-1 300 (1 225,2)
♀♀ 18		177- 800 (252,6)		6	790- 899 (858,0)
Apr.					
♂♂ 21		800-7 200 (2 429,0)		0	—
♀♀ 24		120-1 100 (885,7)		0	—
June					
♂♂ 23		1 030-2 666 (1 192,1)		3	1 256-1 751 (1 435,7)
♀♀ 15		101- 250 (176,5)		3	800- 920 (864,0)
Nov.					
♂♂ 21		927-8 000 (1 954,1)		11	1 211-1 752 (1 089,6)
♀♀ 17		102-1 632 (213,0)		8	700- 998 (881,8)

Table 33

Variation in territory sizes (in square metres) according to biotopes, habitats and season in coastal and inland populations of adult *Chamaeleo namaquensis*. Means are in parentheses.

	N	Dunes		Inland	N	Coastal	River bottom		Inland
		Coastal	N				Coastal	N	
Feb.									
♂♂	0	—	2	1 236-1 246 (1 241)	6	872-1 010 (962)	1	1 109	—
♀♀	0	—	1	890	5	231-250 (237)	2	790-800 (795)	—
Apr.									
♂♂	2	1 416-7 200 (4 308)	0	—	5	1 020-1 931 (1 665)	0	—	—
♀♀	4	500-620 (570)	0	—	6	130-1 011 (284)	0	—	—
June									
♂♂	8	1 200-2 666 (1 846)	3	1 256-1 756 (1 436)	5	1 030-1 800 (1 566)	0	—	—
♀♀	0	—	3	800-920 (864)	5	127-230 (174)	0	—	—
Nov.									
♂♂	4	1 632-3 264 (2 380)	3	1 252-1 752 (1 435)	5	1 030-1 800 (1 436)	5	1 211-1 331 (1 266)	—
♀♀	3	408-816 (611)	0	—	5	132-150 (142)	3	700-800 (759)	—
	N	Gravel plain		N	River	Hummocks		Dune	
		Inland (only)				Coastal (only)	N		
Feb.									
♂♂	1	1 300		5	862-6 800 (2 075)	5		771-1 412 (915)	
♀♀	3	879-899 (889)		9	177-800 (263)	4		237-280 (252)	
Apr.									
♂♂	0	—		9	801-1 015 (874)	5		800-4 121 (1 540)	
♀♀	0	—		10	120-1 000 (256)	4		200-1 100 (463)	
June									
♂♂	0	—		6	1 232-1 601 (1 491)	4		1 200-1 600 (1 470)	
♀♀	0	—		7	101-240 (156)	3		210-250 (230)	
Nov.									
♂♂	3	1 229-1 311 (1 280)		8	927-8 000 (2 209)	4		1 532-1 800 (1 666)	
♀♀	5	927-998 (955)		6	102-190 (152)	3		135-1 632 (667)	

The territorial structure of *C. namaquensis* consisted of a more or less centrally located resting area, usually in a redoubt, but there were no surrounding areas of lesser or greater usage. On waking, chamaeleons patrolled to the border limits and encompassed their entire domain; as the day progressed they proceeded inwards in decreasing patrol courses towards the rest area and night-time retirement. In areas of micro-relief, such as hummocks, the border configuration closely followed the higher ground to an extent that a finger-like projection on such high ground of one chamaeleon's territory intruded into lowlands dominated by another. This system prevailed even on monotonously flat areas, and especially on dunes, where one would suspect territories to be circular, or squarish, since there was no local micro-relief to affect border configuration. There was no overlap of any territories with members of the same or the opposite sex. All ownership disputes, and most courting, were border incidents, and upon completion of courting the contact became a territorial challenge, the 'invading' sex partner being evicted. Usually the larger male territories were surrounded by female territories more than they bordered on those of other males. Female territories were smaller than those of males.

Juveniles had no territories of any discernible sort. They always slept on an object, not necessarily the same, and companionably together when the occasion warranted. Juvenile *C. namaquensis* occupied a shifting home range (10–53 m²; \bar{x} = 27.5) that occurred wholly or partly in the strongly defended territories of the adults, from whom they were free of challenge. Recently hatched *C. namaquensis* initially had their home ranges within the territory of one of their parents, or within the territories of both parents. As they matured, the juveniles apparently began defending their home ranges as they stabilized their locations. By shifting an undefended space when juvenile and free of challenges, the young might find an unoccupied area that they can defend on adulthood.

Establishment of territories was impossible in captivity and this mediated an entirely different type of spatial occupancy in *C. pumilus* and *C. namaquensis*. Both defended favoured rest sites and *C. pumilus* giving birth and ovipositing *C. namaquensis* defended the parturition and nest site, respectively, from all intruders. Thus, in captivity both chamaeleons worked on a 'free run' basis, which, in the case of *C. pumilus* explains why previous authors considered it not to engage in fights, since they had not observed it in the field.

Literature accounts of lizard social organization are virtually limited to American forms, especially the iguanid *Uta stansburiana*. Harris (1964) studied social interactions in an agamid, and noted that female *Agama* in estrous are more submissive to males than non-estrous females. The same was noted in *Chamaeleo pumilus* and *C. namaquensis*, and by Fitch (1940) for *Sceloporus occidentalis*, Irwin (1965) for *Uta stansburiana*, *U. stejnegeri* and *U. hesperis* (Burrage 1966) and demonstrated (Ferguson 1966) as controlled in *Uta* by FSH.

Brain (1961) describes the display of *Chamaeleo dilepis* as similar to that of

C. namaquensis, but *C. dilepis* threatens broadside on, rather than in face-off position as in *C. namaquensis*. Bustard (1958: *C. jacksoni*; 1965: *C. hohnelii*; 1966: *C. bitaeniatus*; 1967: *C. gracilis*) describes the behaviour of several captive specimens, and in his discussion of *C. gracilis* also mentions observations on *Microsaura pumila* (= *Chamaeleo pumilus*) and *Chamaeleo chamaeleon* (= *Chamaeleo chamaeleon*). *C. jacksoni* exhibits ritualized fighting, using its horns to ward off attackers of its own and other species, and in intraspecific conflicts in attempts to dislodge each other. *C. hohnelii* possesses the most highly ritualized fight behaviour, with the use of more extreme colour changes of any other chamaeleon, the combatants circling each other with mock-biting, which settles encounters without injury. Schmidt & Inger (1965) describe display in *C. ituriensis*; submission is by assuming a drab colour, with which the wearer is safe from further attack. The male *C. hohnelii* is the more aggressive sex, with the reverse being true of *C. bitaeniatus*. *C. chamaeleon* and *C. gracilis* have threat display followed by actual fighting, inflicting severe, sometimes fatal, injuries, as is true of *C. namaquensis* and *C. pumilus* in the field. *C. gracilis* has a submissive posture, which secures the chamaeleon assuming it from attack from even an irate individual. In this posture the body is longitudinally extended making the minimal distance between dorsal and ventral areas. Both sexes of *C. pumilus* were observed to threaten other lizards, as Bustard (1965) notes for female *C. hohnelii*. Lateral compression, throat gorging, open-mouthed hissing and aposematic colour and patterns are the norm of chamaeleon display. In especially intense displays, they rock vigorously from side to side. *C. bitaeniatus* (Bustard 1966) and *C. pumilus* (Bustard 1967a) males do not fight and are less aggressive than the females. Bustard's observations as to display and behaviour patterns of *C. pumilus* are essentially as in this study and in most respects as found by Spence (1966) for *Microsaura damarana* (= *Chamaeleo pumilus*) and Von Frisch (1962) for *Microsaurus pumilus* (= *Chamaeleo pumilus*), except Von Frisch considers females less hostile than the males. Unfortunately, all these workers examined *C. pumilus* in captivity, whereas individuals of this species did give combat in the field.

Fighting in wild populations of lizards is rare, but has been recorded for the iguanids *Sceloporus grammicus* (Evans 1946) and *Uta stansburiana* (Burrage 1966; Tinkle 1967). There is no study, other than the results reported here, for *Chamaeleo namaquensis* and *C. pumilus*, on the significance of head-bobbing in chamaeleons at the level of Carpenter's (1962) and Hunsaker's (1962) investigation of the function of this in iguanids. Bustard (1966) found courting male *C. bitaeniatus* jerk the head. The head-bobbing display of *C. namaquensis* bears a close similarity to that which the author observed in the iguanid *Cyclura cornuta*.

Discussions of spatial occupancy in lizards are disconcerting, because of the varied techniques employed, consideration of widely separate populations in different habitats, physical factors, such as varied geologic substrates, local topography, and other biotic dynamics, for example, the population density of the studied species, plant density, and competitors. Also, despite the call for

metrication, a not inconsiderable number of recent papers persist in utilizing outdated units, requiring tedious conversion and a double set of figures in any presentation reviewing data. With few exceptions, no attempt has been made to study adjacent populations in the same general area under slightly different conditions of local topography, geologic substrates, plant, and population density. For example, for five years in Southern California Burrage (1966) observed proximal coastal bluffs, sandy and rocky beaches, coastal and inland canyons, areas of rugged and flat topography and varied geologic substrates, plant density, and population density in an investigation of spatial occupancy of *Uta stansburiana hesperis* and found widely different territory sizes and social organizations obtaining at each study station. Jorgensen & Tanner (1963) used the density probability function obtaining larger territory sizes for this species in Nevada, than did Tinkle, McGregor & Dana (1962) using the minimum polygon method for this species in Texas. Furthermore, in Texas, *Uta* concentrates its activity around wood rat (*Neotoma*) nests in mesquite (*Prosopis*)—a rich source of arthropod prey—and, has less need to wander for food than those in Nevada. Thus, environmental factors in widely separated areas or adjacent areas of varied topography could account for an actual difference in territory size, rather than computation error.

Furthermore, as Tinkle (1967) observes, there are few studies based on large numbers of captures. Indeed, a lack of sufficient minimum recaptures is why no territorial data in April for inland *Chamaeleo namaquensis* are presented here. Most studies demonstrating territorial behaviour in lizards are based on temperate iguanids, with little speculation as to its adaptive significance in reptiles, as has been done by Nice (1941), Hinde (1956) and Carpenter (1958) for other animals, mostly birds. Rand (1967) has made a step in this direction, based largely on his observations of the iguanid *Anolis lineatopus* in Jamaica. Hypothetical values of territory can be: (1) securing a requisite share of environmental resources, and/or (2) mating, and/or (3) survival of the offspring. Rand reports that critical environmental resources for *A. lineatopus* need be defended intra- and interspecifically. In *Chamaeleo pumilus* and *C. namaquensis* food was certainly not critical, especially for the latter. *C. pumilus* defended only its favourite perch for sunning and rest, thus, a secure night-time shelter was critical to this species. The fact that *C. pumilus* was frequently found on top of grass stems in grassy areas away from shrubs cannot be assigned to a surplus, displaced population away from supposed 'choice' shrubs, because wild *C. pumilus* preferred reeds. The high metabolic rate of *C. namaquensis* may require spacing—as their rigid territorialism invokes—for more efficient exploitation of prey. Since *C. namaquensis* has ubiquitous habitat preferences, site selection cannot be important. Vigorous territorial defence for food by male and female *C. namaquensis* seems interesting, particularly when pugnacious defence of territories by both sexes in some lizards (e.g. *Sceloporus merriami*) occurs if food is the limiting resource (Milstead 1961). The structure of territories is possibly most valuable to *C. namaquensis*, for even if transgression was allowed in courting,

it assured that any given male would meet more females than other males during the normal diel patrol of both sexes. Only captives defended the immediate nest site, and such defence must be considered an artifact of captivity. Since suitable nest sites were available in each female's territory, territorial defence in the field would limit or eliminate intrusion of the nest site *per se*. Defence of the nest sites and their location within the female territory prevented exhumation of buried eggs by other females digging a nest.

Bourgat (1968a) notes that each individual *C. pardalis* patrolled an area of several 10 square metres. There are no other comments of territory size in chamaeleons, but defence of a favoured perch is noted for *C. dilepis* (Brain 1961), *C. jacksoni* (Bustard 1958), *C. hohnelii* (Bustard 1965), *C. bitaeniatus* (Bustard 1966), *C. gracilis* (Bustard 1967a), and synonymies of *C. pumilus*, *Microsaurus pumilus* (Von Frisch 1962), *Microsaura pumila* (Bustard 1967a) and *Microsaura damarana* (Spence 1966). All these observations are based on captives, except those of Brain and Spence. Table 34 gives the mean territory and home range sizes of some lizards that are available in the literature. These data used the minimum polygon technique, or planimetry. It is important to an interpretation of chamaeleon home ranges to realize that most chamaeleons are aboreal, whereas the majority of the lizards investigated are terrestrial. Burrage (1966) notes that only the resting site is defended by *Uta stansburiana hesperis* in populations so large (>250 per acre; about >625,0 per hectare) that individual territorial establishment is impossible or unnecessary. In a consideration of territories of *Uta*, Burrage (1966) discusses at length the influence of intricately eroded and/or steep slopes in allowing the establishment of rather large territories in high population densities, which perhaps approaches the spatial relationships of *Chamaeleo pumilus*. This paper also considers local topography, relief, and slope angle, differences in geologic substrates, plant density, and lizard population density at coastal and inland sites in a small geographic area to assess factors regulating the establishment of territories and social organizations in *Uta stansburiana hesperis*.

Knowledge of social behaviour in reptiles is poor; what is known is somewhat confusing, since display patterns appear in newly hatched or newborn young, as observed in *Chamaeleo pumilus*. Carpenter (1967) gives an interesting review of social behaviour of iguanids, with pertinent references, and a detailed study (Carpenter 1961) of social behaviour of the desert iguana *Dipsosaurus dorsalis*. Hunsaker & Burrage (1969) studied a multi-species assemblage of captive iguanids and demonstrated a shift from territories to a social hierarchy as a result of population pressure and reduction of available area. This hierarchical system is established by increasingly vicious fighting, rather than the normal displays, as population pressure increases, and/or the available area is reduced. Similar social hierarchies in wild populations of normally territorial iguanids are noted for *Ctenosaura pectinata* (Evans 1951). Burrage (1966) studied the various social relationships of *Uta stansburiana hesperis* of California in relation to habitat and physical factors, population

Table 34

Review of mean territory and home range sizes of some of the lizards reported in the literature.
Area occupied

Species	Sex/Age	Acres	Metres ²	Remarks	Source
<i>Amblyrhynchus cristatus</i>	♂♂ ad't.	—	1,0	only in breeding season	Carpenter (1967)
	♀♀ „	—	—	only displays	„
<i>Ameiva quadrilineata</i>	♂♂ juv.	—	16,4		Hirth (1963)
	♀♀ „	—	15,1		„
	♂♂ ad't.	—	21,1		„
	♀♀ „	—	13,7		„
<i>Anolis sagrei</i>	♂♂ „	—	> 36,0		Evans (1938)
<i>Basiliscus vittatus</i>	♂♂ juv.	—	14,9		Hirth (1963)
	♀♀ „	—	12,4		„
	♂♂ ad't.	—	12,0		„
	♀♀ „	—	12,2		„
<i>Chamaeleo namaquensis</i>	♂♂ + ♀♀ juv.	—	27,5		this study
	♂♂ ad't.	—	1 717,5	coastal	„
	♂♂ „	—	1 250,2	inland	„
	♀♀ „	—	382,0	coastal	„
	♀♀ „	—	867,9	inland	„
<i>Chamaeleo pardalis</i>	♂♂ + ♀♀ „	„	‘several 10 m ² ’		Bourgat (1968a)
<i>Chamaeleo pumilus</i>	♂♂ + ♀♀ „	—	600,0		this study
<i>Cnemidophorus hyperythrus</i>	♂♂ „	0,07	283,3		Bostic (1964)
	♀♀ „	0,10	404,7		„
<i>Cnemidophorus tigris</i>	♂♂ + ♀♀ juv.	0,09	364,2		Jorgensen &
	♂♂ ad't.	0,50	2 023,5		Tanner (1963)
	♀♀ „	0,24	971,3		„
<i>Ctenosaura pectinata</i>	♂♂ + ♀♀ ad't.	—	2,1		Evans (1951)
<i>Sceloporus olivaceus</i>	♂♂ juv.	0,027	109,3		Blair (1960)
	♀♀ „	0,017	68,8		„
	♂♂ ad't.	0,17	687,9		„
	♀♀ „	0,07	283,3		„
<i>Uta stansburiana hesperis</i>	♂♂ juv.	0,005	20,2	California	Burrage (1966)
	♀♀ „	0,004	16,2	„	„
	♂♂ ad't.	0,05	202,4	Calif. coastal	„
	♀♀ „	0,034	137,6	„	„
<i>Uta stansburiana hesperis</i>	♂♂ ad't.	0,075	303,4	Calif. inland	Burrage (1966)
	♀♀ „	0,056	226,6	„	„
	♂♂ „	0,021	85,0	intertidal home	„
	♀♀ „	0,016	64,8	range of strand-dwellers	„
<i>Uta stansburiana stansburiana</i>	♂♂ + ♀♀ juv.	0,04	161,9	Nevada	Jorgensen &
	♂♂ ad't.	0,10	404,7	„	Tanner (1963)
	♀♀ „	0,03	121,4	„	„
<i>Uta stansburiana stejnegeri</i>	♂♂ „	0,11	445,2	Texas	Tinkle (1967)
	♀♀ „	0,03	121,4	„	„

pressure and food supply. The social organization of other races of *U. stansburiana* have been studied by Tinkle (1967). Clarke (1965) studied several iguanids in captivity, showing formation of dominants-sub-dominants hierarchies. Harris (1964) gives a detailed account of social behaviour in the agamid, *Agama agama*, noting formation of social hierarchies in high population densities. Harris further notes the establishment of territorial borders in *A. agama*, where two males fought several times over a path between their boundaries. Fighting decreased and eventually display along the path replaced combat as the border became established, with rare attempts at violation. Establishment of social hierarchies in high population densities limits the frequency of antagonistic behaviour that would result in attempts at territory formation. This has been demonstrated by Soulè (1964) and Burrage (1966) in the case of littoral and insular high density populations of *Uta*, where only the retreat burrow of each lizard is defended and only a 'free run' home range exists. This has also been noted by the latter author for some inland populations and is always associated with abundant food supplies.

K. Reproduction

1. Sex determination and description of adult *Chamaeleo pumilus* and *C. namaquensis*

Males are the smaller sex in *C. namaquensis* and *C. pumilus*. Male *C. pumilus* have a slightly longer tail length (49–56%; \bar{x} = 53% of total length) than females (39–56%; \bar{x} = 47%). In *C. namaquensis* the tail length never exceeds the snout-vent measurement and tail length as a percentage of total length is nearly equivalent in the sexes (males; 30–44%; \bar{x} = 38%; females; 23–50%; \bar{x} = 38%). In both species the limb proportions are more robust in males, especially the hind, and the head proportionately larger, more rugose and ornamented as compared with females. The tail base of males, housing the paired copulatory organs, is larger and has a distinctly swollen appearance when the animal is reproductively active. The hemipenes can be everted by gentle pressure on the tail base to determine sex at any age.

Zoond & Eyre (1934) describe the general pattern of *C. pumilus* to consist of stripes, patches and individually coloured skin tubercles, arranged as 'bands' (mid-laterum), 'islands' (large tubercles within the bands), 'margins' (dorsal and ventral to the islands), and 'back' (area dorsad of the margins). Bands are always present, though varying in width and distinctness between individuals, and at thermal neutrality (Colour Index '2–3') are orange or brown. The ground colour of the back in adults is usually green, though some have it brown, russet, or yellowish at thermal neutrality, which is essentially a continuation of a juvenile colour type (Table 48). In these individuals, always females, brown predominates and there is really no distinct pattern. The usually blue or gray islands and margins vary and may be totally absent in some, especially females. The margins are quite wide and often intensely bright blue in some males. Some *C. pumilus* have large orange tubercles in the back, or green region. Further discussion of the pattern of *C. pumilus* is given by Zoond &

Eyre (1934) and as they note, it is extremely variable with individuals, and changes somewhat in each through the Colour Index, since each colour, and thus the pattern lay out, is masked, or enhanced through the values of the Colour Index. However, a brown one, for example, cannot go green, or vice versa, but only 'light' or 'dark' phases of these colours; a feat also noted by Farghaly (1941) for *C. vulgaris* (= *C. chamaeleon*) and a host of others back to Aristotle.

The 65 male *C. pumilus* examined varied in snout-vent from 53,0–93,0 mm (\bar{x} = 73,5 mm), with the tail 55,5–107,0 mm (\bar{x} = 82,3 mm). The 86 female *C. pumilus* examined had a snout-vent length of 51,0–102,0 mm (\bar{x} = 78,8 mm), with the tail 52,0–103,0 mm (\bar{x} = 78,0 mm). Spence (1966) collected 4 males and 7 females of *Microsaura damarana* (= *C. pumilus*) at the Storms River bridge in the Tsitsikama National Park, Cape Province. He found the snout-vent length to be 54,6–78,0 mm (\bar{x} = 62,9 mm) in the males; and that of the females to be 51,6–78,3 mm (\bar{x} = 65,8 mm). Tail length for the Tsitsikama males ranged from 125,2–192,5 mm (\bar{x} = 147,7 mm), with the tail 55,4–59,5% (\bar{x} = 57,2%) of the total length, and for the females tail length ranged from 58,5–97,5 mm (\bar{x} = 77,0 mm), with the tail 50,9–55,5% (\bar{x} = 53,6%) of the total length. Since (see pp. 6–7) this study follows Hillenius (1959), it is not known whether the differences in sizes and the tail as a percentage of the total length between Spence's Tsitsikama *M. damarana* (= *C. pumilus*) and *C. pumilus* in the southern Cape Province are ascribable to his smaller sample (i.e. random error), genuine specific, or subspecific differences, or simply a geographic cline within a species. Bustard (1966) noted that the sexes of the viviparous chamaeleons rest differently; the males longitudinally stretched, with the tail straight out; the females hunched, with the tail in an ungripping coiled watch spring.

There are no sexual, or age pattern differences in *Chamaeleo namaquensis*, but there are differences in pattern (Table 35) and proportions between coastal and inland individuals. For example, the depth and breadth of the head of most coastal specimens are almost equal and the body stockier and more porcine, while most inland individuals have a conspicuously long, deep,

Table 35

The percentage of ground colour types in the inland and coastal populations of *Chamaeleo namaquensis* (coastal N = 100; inland N = 40).

Ground colour type	Populations						
	Inland				Coastal		
	Dunes	River bottom	Gravel plain	Shore	Dunes ± 8 km in	River bottom	Gravel plain
Sulphur yellow	—	—	—	80	35	10	2
Reddish	87	15	—	—	15	—	—
Gray	13	85	100	19	20	50	97
Green	—	—	—	1	30	40	1

narrow skull, and the body form and proportions are more attenuated and slender. The tail length as a percentage of the total length also differs.

2. Courting

Courtship was observed in the field and captivity during all months except June and July in *Chamaeleo pumilus* and from April to July in *C. namaquensis*. It is similar in pattern to that described for the African *C. dilepis* (Cott 1934), Trench (1912) for the Indian *C. calcaratus* (= *C. chamaeleon zeylanicus*) and *C. vulgaris* (= *C. chamaeleon*) as described by Schrieber (1912).

C. pumilus courted only in bushes. Courting *C. pumilus* males are a bright green, the females usually dark. In most respects as to head and body motions the courtship of *C. pumilus* closely resembles that given below for *C. namaquensis*, except the former head bobs more jerkily in a flat, horizontal plane. In *C. pumilus* the tail is kept on the branch and there is no circling dance. Presumably this is because courtship occurs in different situations in the two species. Coitus is as described below for *C. namaquensis* and in *C. pumilus* lasts from seven to fourteen minutes. Bustard (1963) observed courting in *Microsaura ventralis* (= *C. pumilus*), with coition lasting up to two hours. Von Frisch (1962) found *Microsaurus pumilus* (= *C. pumilus*) copulated for eleven minutes. During coition the female is passive, but becomes aggressive after coitus, which temperament lasts until termination of her pregnancy. As also observed in the literature cited here on chamaeleon breeding, these animals are solitary, tolerating close proximity only during mating. *C. pumilus* and *C. namaquensis* were seen to copulate two to three times per day, several times per week, and both sexes are even more aggressive to members of their own sex (see population structure p. 105) at such times.

Courting *C. namaquensis* of both sexes are mottled and spotty. The male *C. namaquensis* approaches the female with his tail held up and commences 'dancing' around her with a slow, pronounced weaving side to side of the body; not fast as with the territorial challenge. This is similar to head-bobbing in other lizards, but in *C. namaquensis* the body and head bob in unison, as it were. However, the head concurrently describes a horizontal 'S'-shaped bobbing in challenge, which may evidence itself in initiation of courtship (see p. 101). The large female, if receptive, remains passive, or 'face-offs' the male. Then he intensifies his display with sideways jerks of the head and exaggerates his highly erect 'dancing' stance, lateral body compression, and tail held high. Continuing, both open their mouths and 'biss' at each other, lunging, weaving back and forth, and flicking their tails at each other. If the male touches the female, she may feign biting, but usually prods him with her jaws closed. At the onset of copulation the female bolts a short distance, pursued by the male. The female halts in a highly erect and exaggerated stance, and the male climbs on to her back just anterior to her hind legs, his hind limbs gripping hers on their dorsal surfaces. The plantar surface of the male's fore paws are placed on the front of the female's axilla. The male swings

down his tail under the female's tail base, bringing their vents in apposition. One of the hemipenes is everted and enters the female's cloaca. Copulation lasts for five to fifteen minutes in 'adpressed' Body Compression 'I' and is of the normal saurian pattern.

Sex recognition is by sight in the related iguanids and agamids, and in these, differences in colour, shape and behaviour are used in sex determination. Since size is the only unvarying difference in the chamaeleons studied, it is difficult to know whether this would have any value in sex determination for a large male and a small, recently matured female, or one medium-sized. Mating in chamaeleons may start off as a challenge and the answering behaviour of the female to this determines the outcome. Brain (1961) considered there were frequent rebuffs to homosexual mating attempts due to 'mistakes', with the enraged and unwilling male partner pulling off his attacker. This may be so for the *C. dilepis* Brain observed, but in *C. pumilus* and *C. namaquensis* such injuries were due more to territorial fighting and in these species both sexes had such back scars. Non-receptive females aggressively asserted themselves by biting the inguinal region and flanks of a potential suitor, and since the females are larger than the males, this frequently ended in damaging injuries and death. This occurrence is particularly true in *C. namaquensis*.

Trench (1912) observed copulating *C. chamaeleon zeylanicus* in October, noting mated females were a jet black and aggressive to males. Bons & Bons (1960) say courting occurs in August and September in the North African deserticulous *C. chamaeleon*. Brain (1961) gives a four month gestation period for the East African *C. dilepis*, putting courtship back to about May, agreeing with Milner (1947). Cott (1934) observed *C. dilepis* courting in February in Mozambique.

Only recently ovulated females of *C. pumilus* and *C. namaquensis* were receptive to males, a condition noted in iguanids by Burrage (1966) for *Uta stansburiana hesperis* and *Sceloporus occidentalis* (Fitch 1940).

3. Description of the eggs of *Chamaeleo namaquensis*

Fresh-laid eggs were beige, becoming immaculate white with thin, parchment-like shells, though the sand usually adhering to them gave them a reddish appearance. Of 250 *C. namaquensis* eggs examined (Table 36) in the field and captivity, the largest was $26,0 \times 14,5$ mm, 2,8 g; the smallest $17,5 \times 10,0$ mm, 1,2 g ($\bar{x} = 20,5 \times 11,6$ mm; 1,5 g). FitzSimons (1943) states that *C. namaquensis* eggs average 20×13 mm at laying. *C. dilepis* eggs may be spherical (diameter 8,0–10,0 mm (FitzSimons 1943), 12,5 mm (Wager 1958)) or oval ($12,0-16,0 \times 7,0-8,0$ mm (FitzSimons 1943), $10,8-15,4 \times 7,2-10,6$ mm (Brain 1961)). *C. gracilis* eggs when laid average $10,0 \times 14,0$ mm (Menzies 1958), and Shaw (1960) gives *C. basiliscus* eggs as being $10,0-14,8 \times 9,5-13,5$ mm, 0,7 g ($\bar{x} = 13,3 \times 9,9$ mm; 0,67 g). All in all, there is a dearth of information on chamaeleon eggs as compared with other saurians.

Table 36

Monthly egg-laying data for *Chamaeleo namaquensis* showing size and weights of females before laying their eggs, size and weights of eggs at oviposition, and numbers and size of clutches. Dimensions are in millimetres and weights in grams. 'S-V' denotes snout-vent.

Month	Size of females			N	Clutches size range	\bar{x}	Size of eggs		Weight	$l \times w$ Means	Wt
	s-v	+ tail	Weight				length	+ width Ranges			
May	. . .	106-141	77-86								
June	. . .	106-120	64-96	4	10-15	12,5	18,5-22,0	10,0-12,5	1,2-1,7	20,0	1,5
July	. . .	115-140	55-65	4	12-13	12,5	19,8-21,0	11,0-12,8	1,5-1,7	20,3	1,6
Aug.	. . .	108-115	51-155	4	10-22	13,0	18,0-21,0	11,5-13,5	1,4-1,7	19,7	1,6
Sep.	. . .	90-143	72-86	3	10-12	11,7	17,5-24,0	10,0-14,5	1,2-2,8	19,6	1,7
				4	6-13	9,5	18,0-26,0	10,0-13,0	1,2-1,9	21,4	1,5

4. Parturition sites of *Chamaeleo pumilus* and nesting sites of *Chamaeleo namaquensis*

Chamaeleo pumilus females giving birth select small-leaved shrubs or grass stems. Parturition of 56 litters for a total of 614 young was observed. In any given litter, time between births of young took less than a second to as much as 13 minutes (\bar{x} = 8 min, 10 sec). The time between parturition and the young being active and free of their membranes was usually immediate. About 10% were born internally, appearing free of their egg membranes and exhausted yolk sacs, which came out first. The entire birth process may take nearly two hours for a litter complement of 10 or more young, or as little as twenty minutes for a litter complement of 5 or less. Abel (1931) found *C. pumilus* and *C. melanocephala* (= *C. pumilus*) to give birth to nine young in one and a quarter hours. Bustard (1955, 1965, 1966) records and compares birth in several viviparous chamaeleons, including *C. bitaeniatus*, *C. hohnelii*, *Microsaura pumila* and *M. ventralis* (= *Chamaeleo pumilus*). Nine *Chamaeleo pumilus* young freed themselves and were active in a minute, six *C. bitaeniatus* were free in 1,3 minutes, but *C. hohnelii* took 5,3 minutes. Bustard (1955) gives the entire birth process of seven *C. pumilus* as lasting 24 minutes, with the average time of the birth process of individual young as 1 minute, 42 seconds (range: 0,15 sec to 4 min) and the average time between births of individual young as 2 minutes, 50 seconds (range: 0,04 sec to 7 minutes, 15 seconds).

Chamaeleo namaquensis nests were constructed in the typical oviparous chamaeleon manner, consisting essentially of a hole large enough for the female with a terminal enlargement for her to turn around in at the end of excavation and commencement of egg-laying. In the field favoured nest sites were loose gravel, and especially the foot of and the windward slopes of large dunes, and below the crest of small (6 m high) ones. Such sites were abundant in the field, and each female had its own nesting site located within its tightly defended territory. In crowded, captive conditions an area 350 mm in diameter was viciously defended against intrusion by other females, gravid or not, and even males. For up to a week prior to laying, most females dug exploratory holes to a depth of 130 mm; which, presumably, was in search of the layer of moist sand under which the eggs were laid. In captivity, the eggs were laid at 100 mm total depth, provided an artificial layer of saturated sand was available.

The construction of six nests in captivity for a total of 83 eggs was observed, and two nests in the field for a total of 25 eggs. Only data in Table 36 refer to the 225 eggs laid in captivity. Nest-building in captivity was as in the field, and the process was observed by inserting a horizontal glass viewing plate, under which the animals dug. Some completed nests were excavated to examine their form. After preliminary holes had been dug, the preferred site was selected, usually on a slight rise, since a steep slope would invite tunnel collapse in digging, especially through the initially dry, non-cohesive upper substrate layers. Nevertheless, the top portion of the nest was about 300 mm in diameter, plus a spoil heap of 1,20 m. The nest was constructed as a pit down to the loose, moist sand layer, which was 10 mm subsurface in gravel, deeper for dune

sand, and extended for a depth of approximately 150 mm, becoming dry deeper than this. It was to this dry layer below the loose, moist layer that *C. namaquensis* dug. Excavation through the moist area was narrow (approximately 150 mm wide) and the terminal enlargement in the dry area beneath this was 77 mm or more, so that the nest had an appearance of a wide-mouthed, beakered flask, with a narrow neck and wide base. Dug at an angle of 60–80°, the nests were almost consistently of an overall depth of 200–250 mm, rarely more, never less. The female excavated this with her eyes closed by using her head as a battering ram, pushing vigorously forwards and laterally, and somewhat up and down. The right fore and left hind feet acted as braces, while the left fore foot dug, pushing the excavated spoil back to the right hind foot for evacuation. This arrangement was alternated back and forth in the course of excavation. As the spoil accumulated behind, the female cleared this by backing up and using the hind feet as ploughs until at least 350 mm clear of the excavation area, where the spoil was dumped on the heap. At the top of this heap, the female shook off the spoil that had accumulated on the top of her head, then opened her eyes and walked back to more excavating. Nest excavation occurred at any time of the day or night. The time from the start of excavation to completion of oviposition took as little as eight or as long as ten hours, with no rest between excavation and oviposition.

The first eggs were laid with the female facing tail outward, positioning the dropped eggs with her fore feet as they rolled from her cloaca under her body and down to the terminal enlargement. In ovipositing the tail was held up as space permitted, the pelvis resting on the floor, and the legs held high and far apart, especially the hind ones. Passage of eggs resembled defecation. Six to eight eggs were well-spaced in the loosened floor of the terminal enlargement and constituted the first layer of eggs, which was then covered by spoil and then another layer of eggs and so on. As the terminal enlargement filled, the female reversed her position and with the head then pointing outward completed egg-laying, each egg layer being separated from that above and below it by a layer of spoil. The final layers were positioned with the hind legs, and the upper spoil layer tamped down. The first eggs were laid at average intervals of 20 minutes, which became progressively shorter as laying proceeded. At mid-laying the interval between eggs averaged 10 minutes, 7 minutes towards the end, and to as little as 30 seconds or almost instantly for the last dropped. Depending on the clutch complement, one or two hours comprised the ovipositing period. Upon emerging at the conclusion of egg-laying, the female used her hind legs to push spoil back into the hole to fill it. This final operation proved interesting in captivity, since other *C. namaquensis* of both sexes sometimes assisted. Spent females ate to capacity and captives must be given as much food as desired.

Chamaeleo basiliscus (Shaw 1960), *C. chamaeleon zeylanicus* (Trench 1912), *C. dilepis* (FitzSimons 1943; Milner 1949; Wager 1958; Brain 1961) and *C. gracilis* (Menzies 1958) all construct nests as does *C. namaquensis*, except that

those of *C. dilepis* are at a less steep angle (45°) and may be considerably deeper (250–700 mm), as those of *C. chamaeleon zeylanicus* (to 350 mm), or considerably shallower (85 mm) as those of *C. gracilis*. Digging time may be as much as 60 hours (*C. chamaeleon zeylanicus*), 44 hours (*C. gracilis*), or 24–30 hours (*C. dilepis*). Rain-moistened soil is selected for ease of digging in these species, and in the case of tropic forms construction of nests coincides with the end of the rainy season.

5. *Annual number and size of litters of Chamaeleo pumilus and clutches of C. namaquensis*

Sexually mature *C. pumilus* females had four litters per year; the size of the female bears some relation to litter size, and the larger females had the largest litters (Tables 29, 37, 38). The first litter (7–9; \bar{x} = 8) of newly matured females (snout-vent 51–60 mm) was larger (3,0–6,0; \bar{x} = 5,1) than that of those 61–70 mm snout-vent. Births have been recorded in February to May, September, November, and December. The largest litters (5,0–21,0; \bar{x} = 17,0 young) were born in December; the smallest in April (3,0–6,0; \bar{x} = 4,5), overall; 3,0–21,0 (\bar{x} = 11,0). The difference in size of the young, according to parturition month, is discussed later.

Table 37

Number of embryos and developing oviducal eggs per month in relation to the snout-vent length of female *Chamaeleo pumilus*. (Means are in parentheses.)

Month	Snout-vent length in millimetres					
	51–60	61–70	71–80	81–90	91–100	101–110
Feb.	7		8–13 (10,5)	11–16 (13,5)	18	
Mar.		3–5 (4,6)	11	6–15 (13,3)		
June			18	21		
July			13	7–18 (12,5)	12–13 (12,5)	17
Aug.			12	12		
Sept.		6	7–10 (8,5)	18		
Oct.	9		11–16 (13,5)		19	
Dec.			10–11 (10,5)	14		
Jan.		5	11	10		

Table 36 gives the size of female *Chamaeleo namaquensis*, the size of clutches laid by each, and all other pertinent data. *C. namaquensis* eggs have been recorded from May to September. Regardless of the size of the laying female, the clutch complement was largest in those laid in July (10,0–22,0; \bar{x} = 13,0) and smallest in those of September (6,0–13,0; \bar{x} = 9,5). The majority of those laying in September were recently matured females, though considerably larger and older females laid the same number (Table 39). The overall clutch complement was 6,0–22,0 (\bar{x} = 13,2). September clutch eggs were slightly larger (18,0–26,0 \times 10,0–13,0 mm; 1,2–1,9 g; \bar{x} = 21,4 \times 11,3 mm; 1,5 g) than those of other months (Table 36). Females laid two to three, possibly four clutches per year (Tables 30, 40).

Table 38

Monthly birth data for *Chamaeleo pumilus* showing pre-parturition size and weights of females, offspring size and weights at parturition, and litter complements. Sizes given in millimetres; weights in grams. (See Table 46 for pattern and sex analyses of newly born young.)

Month	Size of females			N	Litters Size Range	\bar{x}	Size of offspring			Wt.
	s-v + tail Ranges	Wt. Ranges	s-v + tail Means				s-v + tail Ranges	Wt. Means		
Feb.	. . . 51-99	7.4-22.5	78.7	12	5-18	11.8	20-24	22-27	22.0	0.4
Mar.	. . . 70-87	9.4-17.6	81.2	14	5-15	9.7	19-24	19-22	21.8	0.3
Apr.	. . . 51-62	5.0-10.0	56.5	4	3-6	4.5	20-24	23-26	22.0	0.4
May	. . . 53-70	6.2-14.0	67.7	6	3-9	6.0	19-24	19-23	22.0	0.3
Sept.	. . . 75-77	17.5-22.0	76.0	6	14-15	14.3	17-26	16-26	20.5	0.32
Nov.	. . . 76-80	19.0-22.0	77.7	8	8-16	11.8	22-27	20-26	24.7	0.35
Dec.	. . . 50-99	8.0-24.0	70.3	6	5-21	17.0	20-24	22-27	22.0	0.4

FitzSimons (1943) gives a clutch size of 20 eggs for *Chamaeleo namaquensis*. Clutch size in other oviparous chamaeleons varies from 10 in *C. chamaeleon zeylanicus* (Minton 1966) and *C. dilepis* (Brain 1961) to as many as 31 in *C. chamaeleon zeylanicus* (Trench 1912) and 45 in *C. gracilis* (Menzies 1958), and as high as 57 in *C. dilepis* (Wager 1958). The average clutch complement of oviparous chamaeleons is 30-40.

Table 39

The monthly number of oviducal eggs and yolked ovarian follicles at or greater than five millimetres in diameter in relation to the snout-vent length of female *Chamaeleo namaquensis*. Means are in parentheses.

	Snout-vent length in millimetres					
	81-90	91-100	101-110	111-120	121-130	131-140
Apr.						
Oviducal eggs	5			13		
Ovarian						3
June						
Oviducal eggs			10			
Ovarian			14	2	11	
Aug.						
Oviducal eggs			10			
Ovarian			14	2	12	
Nov.						
Oviducal eggs						
Ovarian	7			2	8-13 (10.5)	
Feb.						
Oviducal eggs						
Ovarian	10	20	15			25

Table 40

The growth and reproductive states in captivity of five male and five female *Chamaeleo namaquensis*. Dimensions are in millimetres; weights in grams.

Sex	April			August			November		
	s-v + tail	Wt	Rep.	s-v + tail	Wt	Rep.	s-v + tail	Wt	Rep.
♂♂	105 77	43	IBL	108 80	50	IBL	115 82	52	IBL
♂♂	97 84	37	IBL	101 88	42	IBL	112 100	51	IBL
♂♂	135 72	50	IBL	136 82	54	IBL	140 103	66	IBL
♂♂	120 70	45	IBL	123 73	47	IBL	130 75	54	IBL
♂♂	75 55	13	IBL	86 58	18	IBL	90 60	27	IBL
♀♀	108 90	50	GR	110 90	57	GR	110 90	62	LYF
♀♀	127 85	85	GR	132 71*	89	GR	135 72	113	GR
♀♀	117 83	70	GR	120 90	60	LYF	121 100	51	SYF
♀♀	86 85	47	GR	100 70	61	LYF	109 92	81	GR
♀♀	82 78	45	GR	98 80	40	SYF	101 89	49	LYF

* = Part of tail bitten off in a territorial dispute over an egg-laying site with another female.

s-v = snout-vent

Wt = weight

Rep. = reproductive state

IBL = in bloom (♂♂ only)

GR = gravid (oviducal eggs)

SYF = small yolked follicles (<5 mm diam.)

LYF = large yolked follicles (>5 mm diam.)

Oviparous chamaeleons lay far more eggs than saurians of comparative size or slightly larger (Mayhew 1968), including the closely related agamids. This prolificity is shared by viviparous chamaeleons. *C. pumilus* was found to have litter sizes as high as 21 young as did Spence (1966) for *Microsaura damarana* (= *C. pumilus*). Of viviparous chamaeleons, the overall average of young per litter is about 10, according to data from this study, Abel (1931), FitzSimons (1943), Atsatt (1953), Bustard (1955, 1963) and Von Frisch (1962). Three is the smallest recorded litter size, agreeing with this study. Angel (1933) records a maximum litter size of 20 for *C. leikiensis* (= *hohnelii*), with an average of 12-13; and Bustard (1965) gives a litter size of 8,0-11,0 ($\bar{x} = 10,0$) for *C. hohnelii*. *C. bitaeniatus* has litters of 3,0-25,0 ($\bar{x} = 17,3$) young (Bustard 1966).

6. Success of the litters of *Chamaeleo pumilus* and the clutches of *Chamaeleo namaquensis*

Predation on eggs has never been recorded, but ants and burrowing insect larvae may be a potential threat to *Chamaeleo namaquensis* eggs. Some females did dig an extension to their retreat burrows for laying their eggs, and the continued presence of the adult in such instances might convey a measure of protection. Fitch (1956) felt the iguanid *Crotaphytus collaris* to suffer a high nest mortality with some potential clutches not being represented by any hatchling. In the field all the potential clutches of *Chamaeleo namaquensis* (Table 30) and the litters of *C. pumilus* (Table 29) were represented. In the case of *C. namaquensis* there appears to be evidence of a fourth clutch (Table 30). However, it is better to consider this (Table 30) the first clutch of newly matured individuals, since confirmation is lacking of any one marked female having four clutches a year.

Clutch and litter success are complexly intermeshed with such factors as weather, gestation, incubation, predation on gravid or pregnant females, growth of the recently hatched or newborn young, and availability of food for the young. In oviparous forms rainfall is very crucial to the success of certain clutches (cf. Burrage 1966, for the iguanid *Uta stansburiana hesperis*, and Mayhew 1968, for all desert saurians), as unseasonal rains seem to destroy nests or promote spoilage of the eggs, though, in fact, most desert saurian eggs quickly shrivel up in dry sand and need direct application of water, maintenance of 100% humidity being insufficient. However, nests of *U. s. hesperis* exhumed towards the end of incubation are quite dry, though moistness prevailed at laying and during early incubation. Thus, on a purely meteorological basis, the second and third clutches of this iguanid are the most likely to hatch. The *Chamaeleo namaquensis* observed inhabits an area of scant and erratic rainfall, though considerable moisture from fog condensate was closely associated with the eggs throughout the entire incubation period. It would be interesting to know the moisture relations of those eggs of *C. namaquensis* laid outside the fog belt.

7. Role of fat bodies

The work of Harris (1963) on the anatomy of *Agama agama* was applicable for use with chamaeleons. *Chamaeleo pumilus* and *C. namaquensis* have a four-lobed fat body, consisting of two small ventral and two large dorsal lobes, all connected at their posterior ends to the pelvis. Hahn & Tinkle (1965) demonstrated the role of these fat bodies in the ovarian follicle development of the iguanid *Uta stansburiana*. Their significance to the males, which are also subject to cyclical fat body changes, has not been investigated. Hahn & Tinkle showed that ovariectomy in *Uta* eliminated rapid lipid mobilization from the fat bodies, which occurred in those sham-operated. Fat body excision in early estrous *Uta* females induced a high incidence of follicular atresia, and retarded the yolk deposition rate. In pre-estrous *Uta* females follicular growth is delayed or inhibited by fat body excision. The extractable lipid in pre-estrous fat bodies is nearly equivalent to the lipid content in a typical clutch of eggs. Hahn & Tinkle concluded that the adaptive value of the fat bodies is associated with the formation of the first egg clutch, which is the most important.

Tables 41 and 42 for *Chamaeleo pumilus* males and females, respectively, and Tables 43 and 44 for *C. namaquensis* males and females, respectively, and Table 48 for juvenile *C. pumilus* and *C. namaquensis* show the fluctuation in fat bodies according to the reproductive state. It will be noted that in the males fat body size was greatest at those times the testes were active. In *C. namaquensis*, females with developing follicles had the largest fat bodies, and those reproductively quiescent or about to oviposit, the smallest. They follow the pattern of utas. Fat bodies were larger in female *C. pumilus* with embryos over 10 mm snout-vent and with yolking follicles, especially those in excess of 5 mm diameter. Thus, the fat bodies of *C. pumilus* would appear to have a dual role, lipid mobilization for follicle development, and possibly sustenance of the embryos in the later stages of pregnancy.

Fat body excision in four male *C. pumilus* and four male *C. namaquensis* resulted in a decline of testicular activity. Controls which had been sham-operated were unaffected. For four female *C. namaquensis* the results were as for female uta. In six female *C. pumilus*, results on follicular development were as for *C. namaquensis*, and in pregnant ones, only those with very late term foetuses (i.e., near birth) completed delivery of young. For the others, fat body excision resulted in the termination of pregnancy, abortion or resorption of the embryos.

It appears that fat storage in chamaeleons and utas is primarily for reproduction, whereas deserticolous gekkonids store sufficient caudal fat in four days of food ingestion to sustain them for up to nine months (Bustard 1967c).

8. Nature of gonads (adult non-reproductive)

Gonadal state was determined macroscopically and by microscopic examination of serial sections of organs. Inactive testes presented a flattish or squashed appearance externally, and internally the organ was somewhat

transparent, as the epithelium of the tubules was thin and they were loosely convoluted. Sperm ducts not containing semen were thin, whitish to opaque, and wavy to moderately convoluted. Inactive males had a markedly less swollen tail base. In June and July *Chamaeleo pumilus* had inactive testes (Table 41), though in the former month semen was present in the distal part of the sperm duct. In July and August there was no semen in the distal part of the sperm duct, though in August 95% of the males had active testes. In *C. namaquensis* inactive testes were predominant (75%) only in August (Table 43), though all males sampled had semen in the distal part of the sperm duct.

9. Nature of gonads (adult reproductive)

Reproductively active testes occurred from August to May in *Chamaeleo pumilus*, and from February to April, June to August, and in November in *C. namaquensis* in the field and from April to November in captivity. These data suggest virtually reproductively active testes throughout the year in *C. namaquensis*, and it is probably the method of sampling that makes it appear discontinuous. Active testes were robust and spherical in external appearance. Internally, they were yellowish with tortuously convoluted tubules with thick epithelium. Active testes weighed more than twice those inactive. In active males the sperm ducts were white, thickened, and tortuously convoluted, and the tail base was much swollen. In reproductively active *C. pumilus* (Table 41) 100% testicular activity was recorded in all months but April (30%), May (50%) and August (95%). The occurrence of testicular activity in April and May indicates a secondary peak before winter quiescence. Apparently there were a few (Table 29) active males in June amongst the undissected marked population, but these might have had semen in the distal parts of the sperm ducts and inactive testes.

In *C. namaquensis* males (Tables 40, 43) 100% had reproductively active testes, except for August (25%), though 100% had semen in the distal parts of the sperm ducts, except for November when 90% had semen in the distal parts of their sperm ducts and all had active testes.

Yolked follicles were present in *C. pumilus* throughout the year (Table 42). Yolk was deposited in follicles of 2 mm diameter, proceeding to and held at 4 mm diameter if oviducal embryos were present, as in all months, but April, May and November. Yolking of follicles for the next litter was deferred until the oviducally developing litter had at least reached pholidosis. Ovulation occurred at a mean follicle ($N = 157$) size of $7.0-8.0 \times 6.0-6.5$ mm.

In *C. namaquensis* (Tables 37, 39, 44) yolk deposition began with follicles of 2 mm diameter. In both species non-yolked follicles were from 0.5 to 2.0 mm in diameter, and a pearly white. There were no yolked follicles in the February (50%) and November (20%) samples of female *C. namaquensis*. Yolked follicles from 2.0 to 5.0 mm diameter were found in every sample month. In *C. namaquensis* ovulation occurred at a follicle size of 13 mm or

Table 41

Monthly condition of adult male *Chamaeleo pumilus* showing fat body weights, testes weights and dimensions, and the productive state of the testes and sperm ducts. Means are in parentheses.

Month	N	Fat bodies Weight (g)	Testes Weight (g)	Size (mm)	Testes		Sperm duct with semen distally
					Active	Inactive	
Feb.	3	0,005-0,319 (0,122)	0,036-0,084 (0,042)	5,0-7,0 × 3,0-5,0 (6,1 × 4,3)	100%	0%	100%
Mar.	6	0,045-0,305 (0,152)	0,009-0,078 (0,033)	3,0-7,0 × 2,0-4,8 (5,4 × 3,6)	100%	0%	100%
Apr.	8	0,004-0,051 (0,028)	0,015-0,034 (0,023)	4,5-7,0 × 2,0-4,0 (5,4 × 3,0)	30%	70%	100%
May	8	0,002-0,056 (0,026)	0,018-0,046 (0,031)	4,0-6,5 × 2,5-4,0 (5,0 × 3,3)	50%	50%	100%
June	6	0,001-0,214 (0,067)	0,014-0,047 (0,032)	3,5-7,0 × 2,5-4,5 (5,1 × 3,5)	0%	100%	20%
July	5	0,001-0,065 (0,023)	0,017-0,057 (0,031)	4,0-6,0 × 3,0-4,5 (4,8 × 3,5)	0%	100%	0%
Aug.	8	0,009-0,026 (0,018)	0,012-0,045 (0,026)	3,5-6,0 × 2,5-4,5 (4,6 × 3,5)	95%	5%	0%
Sept.	5	0,004-0,024 (0,015)	0,021-0,037 (0,028)	4,0-6,0 × 2,5-4,5 (5,0 × 3,5)	100%	0%	95%
Oct.	3	0,050-0,119 (0,074)	0,030-0,064 (0,047)	5,5-6,5 × 4,0-5,0 (6,0 × 4,5)	100%	0%	100%
Nov.	5	0,002-0,122 (0,049)	0,001-0,029 (0,011)	3,0-6,5 × 2,0-4,0 (4,8 × 3,0)	100%	0%	100%
Dec.	4	0,007-0,127 (0,046)	0,015-0,029 (0,020)	4,5-6,0 × 3,0-4,0 (5,3 × 3,5)	100%	0%	100%
Jan.	4	0,004-0,017 (0,010)	0,015-0,054 (0,033)	4,0-6,8 × 2,5-4,0 (5,3 × 3,3)	100%	0%	100%

Size of adult males examined: body weight 2,8-14,8 g \bar{x} = 8,7; snout-vent 53,0-93,0 mm \bar{x} = 73,5; tail 55,5-107,0 mm \bar{x} = 82,3.

Table 42

Monthly condition of adult female *Chamaeleo pumilus* showing fat body weights (in grams), reproductive state of ovarian and oviducal structure expressed as a percentage of the sample, and numbers of developing oviducal eggs and embryos. (Means are in parentheses: 'S-V' denotes snout-vent. Yolked follicle sizes given are diameters.)

Month	N	Fat body weight	Percentage with embryos		Oviducal		Number of eggs or embryos		Percentage with follicles		Corpora lutea
			≥ 10 mm	< 10 mm (s-v)	Left	Right	yolked	not yolked			
Feb.	6	0,042-0,547 (0,232)	80,0	20,0	4-12 (6,8)	4-10 (6,4)	0,0	20,0	80,0	100,0	
Mar.	6	0,002-0,417 (0,209)	100,0	0,0	2-8 (5,6)	2-7 (4,8)	0,0	20,0	80,0	100,0	
Apr.	9	0,002-0,285 (0,105)	0,0	0,0	0	0	11,1	88,8	11,1	11,0	
May	8	0,004-0,291 (0,131)	0,0	0,0	0	0	37,5	61,5	25,0	0,0	
June	10	0,009-0,140 (0,065)	0,0	40,0	9-12 (10,5)	9	20,0	20,0	40,0	40,0	
July.	10	0,006-0,255 (0,072)	0,0	90,0	4-9 (6,7)	3-10 (6,7)	28,6	0,0	71,5	90,0	
Aug.	7	0,009-0,082 (0,041)	0,0	40,0	5-6 (5,5)	6-7 (6,5)	0,0	80,0	20,0	40,0	
Sep.	7	0,002-0,162 (0,050)	0,0	66,8	3-10 (5,0)	3-8 (5,2)	16,7	33,4	66,8	66,8	
Oct..	7	0,001-0,381 (0,150)	42,9	14,1	4-9 (6,8)	5-10 (7,0)	0,0	42,9	57,1	71,5	
Nov.	5	0,034-0,161 (0,101)	0,0	0,0	0	0	0,0	80,0	20,0	40,0	
Dec.	6	0,023-0,145 (0,074)	16,7	40,1	5-7 (6,0)	5-7 (6,0)	16,7	50,1	33,4	56,8	
Jan.	5	0,008-0,048 (0,023)	20,0	60,0	2-5 (4,3)	3-6 (4,7)	0,0	20,0	80,0	100,0	

Size of adult females examined: body weight 2,1-27,3 g \bar{x} = 11,8; snout-vent 51,0-102,0 mm \bar{x} = 78,8; tail 52,0-103,0 mm \bar{x} = 78,0.

Table 43

Condition by month of adult male *Chamaeleo namaquensis* showing fat body weights, testes weights and dimensions, and reproductive state of the testes and sperm ducts. Means are in parentheses.

Month	N	Fat body weight (g)	Weight (g)	Testes		Testes		Sperm duct with semen distally
				Size (mm)	Active	Inactive		
Apr.	5	0,002-0,119 (0,036)	0,051-0,282 (0,136)	5,0-11,0 × 4,0- 7,5 (8,1 × 6,0)	100%	0%	100%	
June	9	0,003-0,752 (0,270)	0,015-0,259 (0,173)	4,5-11,0 × 3,0- 9,0 (7,6 × 6,1)	100%	0%	100%	
Aug.	4	0,018-0,090 (0,048)	0,067-0,215 (0,165)	8,0-12,0 × 6,5- 9,0 (10,2 × 7,7)	25%	75%	100%	
Nov.	6	0,014-0,542 (0,171)	0,041-0,291 (0,141)	6,0-12,5 × 4,0- 9,0 (9,2 × 6,6)	100%	0%	90%	
Feb.	6	0,030-0,518 (0,215)	0,224-0,438 (0,300)	10,0-13,0 × 6,5-10,0 (11,9 × 8,0)	100%	0%	100%	

Size of adult males examined: body weight 11,7-90,1 g, $\bar{x} = 48,2$; snout-vent 75,0-158,0 mm, $\bar{x} = 112,6$; tail 46,0-105,0 mm, $\bar{x} = 74,9$.

Table 44

Condition by month of adult female *Chamaeleo namaquensis* showing fat body weights (in grams), reproductive state of ovarian and oviducal structures expressed as a percentage of those sampled, and numbers of developing oviducal eggs (Means are in parentheses: 'S-V' denotes snout-vent.)

Month	N	Fat body weight	Oviducal		Mean		Ovarian		Corpora lutea
			Percentage with eggs	number of eggs	percentage having	no yolked follicles			
				left	right	≥ 5 mm diam.	< 5 mm diam.		
Apr.	9	0,013-0,654 (0,264)	33,3	6	7	33,3	100,0	0,0	33,3
June	14	0,059-2,059 (0,928)	28,6	5	5	75,0	50,0	0,0	25,0
Aug.	5	0,057-0,076 (0,064)	60,0	5	5	66,6	33,3	0,0	33,3
Nov.	11	0,027-0,261 (0,113)	0,0	0	0	60,0	40,0	20,0	0,0
Feb.	11	0,126-2,326 (0,927)	0,0	0	0	50,0	0,0	50,0	0,0

Size of adult females examined: body weight 25,2-106,5 g; \bar{x} = 60,8; snout-vent 88,0-140,0 mm, \bar{x} = 119,6; tail 61,0-95,0 mm, \bar{x} = 78,3.

greater in diameter, the eggs being held in the oviducts (see gestation, p. 131) until laying (Table 36).

When eggs were absent, *C. namaquensis* oviducts were silvery-white, thick and crumpled; the distinct crumpled portions were similar to the incubation chambers of viviparous forms (see *C. pumilus* discussion, p. 131) and are called uterine chambers by Kasturirangan (1951). Oviducal eggs (Table 39) were found in the April, June and August samples (see also gestation, p. 135). While oviducal eggs were present, follicle yolking was held at a maximum of 4 mm diameter. When the oviducal eggs were being shelled or laying imminent, development of the next clutch proceeded.

In *C. namaquensis* there was a distinct ovarian follicular and oviducal development cycle. This was also a right-left offset cycle. That is, at one period the right side had more oviducal than ovarian eggs, with the reverse situation being true of the left side. This condition shifted for the next clutches under development, with the left side having more oviducal and less ovarian eggs. *C. pumilus* had an identical right-left offset cycling of developing embryos and follicle development.

Intra-abdominal migration of ova occurred in *C. pumilus* and *C. namaquensis*, but was not common in either. While this phenomenon in other reptiles is recorded for xantusiids, iguanids, and teiids (Mayhew 1968), it is based on the number of oviducal eggs and the occurrence of full-term or regressing corpora lutea for each side. In the chamaeleons observed this method was somewhat inaccurate, as these ovarian structures were sometimes discernible for nothing apparent in either oviduct, and vice versa, which may indicate regression of ovarian structures and resorption of those in the oviduct to which they were related at different paces. Hard yolk sacs bearing no trace of embryos were the only oviducal structures that could not be matched to any corresponding ovarian structure.

Saurian testicular cycles resemble those of birds, and the most common saurian testicular cycle is: (1) with spermatogenesis in late summer and autumn, occurring also during winter hibernation, with spermiogenesis taking place largely in spring, but it may occur in autumn or winter. Mature sperm enter the epididymides, and copulation usually occurs in spring; or, (2) some maintain testes and sexual accessories at maximum through the summer; or, (3) those at the extremes of their (northern) range are biennial in both sexes. Very little is known of tropical forms, and most of the knowledge is based on temperate species, especially the northern varieties.

Food, weather and moisture are some mediating effects of the cycle. Photoperiod effects are hard to gauge, since reptiles expose or shield themselves to and from light in controlling their body temperatures. Licht, Hoyer & Van Oordt (1969) found male *Lacerta sicula* and *L. muralis* to be stimulated by warmth. Licht & Basu (1967) found that *Uma scoparia* testes *in vitro* can produce reproductive products at 37 C, and do not degenerate until held at 44 C. Body temperatures of 44 C are reached by this species in summer when they are

maximally active reproductively and otherwise. Thus, male *Uma* can produce reproductive products at temperatures far higher than can other vertebrates, including desert birds (Riley 1937), which are capable of spermatogenesis only in the cool of night. Mayhew (1967) has shown that apparently the amount of soil moisture during winter determines the breeding of *Uma*. Where this places *C. namaquensis* in this regard is not known, for certainly it was subject to as extreme environmental temperatures as *Uma*, but maintained lower body temperatures. Perhaps of importance here are the lung diverticula (Fig. 12) which surround the gonads in both sexes.

A problem of deciding on reproductive cycles, if any, in chamaeleons (and perhaps other saurians) is the ability of the females of some species to store sperm. The loci of sperm storage is variable, being the anterior segment of the 'vagina' in the iguanids *Callisaurus*, *Crotaphytus*, *Holbrookia*, *Phrynosoma*, *Sceloporus*, *Urosaurus* and *Uta*, the tube between the oviduct and infundibulum in the gekkonids *Coleonyx* and *Phyllodactylus* (Cuellar 1965), and the distal part of the oviduct in *Chamaeleo basiliscus*, *C. chamaeleon* and *C. lateralis* (Saint Girons 1962), and in *C. pumilus* and *C. namaquensis* (this study). Such structures contain large numbers of spermatozoa in females isolated from males for several months, permitting production of one or more fertile clutches or litters. As Cuellar observes, sperm storage permits an effective lengthening of the period of fertile egg-laying.

Little value for sperm storage in *C. namaquensis* can be seen, since the males were reproductively active throughout the year, the sex ratio was almost equal, and both sexes were readily available spatially and temporally to each other. In *C. pumilus* sperm storage has a decided value, especially for the first litter in September of the reproductive year. Cape winters feature considerable rain and quite low temperatures from June to at least October, though such inclement weather may begin as early as the end of April and persist into mid-December. Males were totally inactive in July and August, thus sperm storage in *C. pumilus* females guarantees the first litter and possibly the last, independent of the availability of sexually active males at those times.

Data on viviparous chamaeleons show that *Chamaeleo pumilus* is generally credited with rarely more than one birth per year, corresponding to the Southern Hemisphere summer (FitzSimons 1943; Von Frisch 1962; Bustard 1963; Spence 1966), but only Wager (1958) agrees with this study that litters are multiple, being recorded in February to May, September, November and December. Bustard (1966) records *C. bitaeniatus* births in April, May, July and September to November, and *C. hohnelii* births in August and September (Bustard 1965). Busack & Busack (1967) record November and February births for *C. pumilus*, and Atsatt (1953) February to May, July and November. However, almost all of these records are based on captives, and Atsatt's records of November, April and May 'births' are due to injection with pituitrin of a single female *C. pumilus*. This study's records are of individuals in the field, supplemented with data on captives.

Fig. 12A-C.

The lung, air sac relationship to gonads in *Chamaeleo namaquensis* (A-B) and *C. pumilus* (C).

A. Lung (part between '8' and '11' on mm rule) at expiration shown to the top of black small intestine, and anterior to right ovary. Note large yolking follicles in both ovaries; large white stomach to right of left ovary, and juncture with small intestine and its black visceral peritoneum.

B. Lung (centre left above black small intestine) at almost full inspiration, totally obscuring ovary, which is forced dorsally and medially. (The fat bodies, very large in this female, have been partially excised to improve visibility of other structures.) Especially note transparent (clearer in Fig. 12A) abdominal peritoneum of this species. (Anterior is to left in this photo.)

C. Male *C. pumilus* (anterior to right) with lung at almost full inspiration, almost obscuring right testis, which is abnormally lacking a black visceral peritoneum and appears white. Its opposite number, just posterior to (normal position of gonads), and below it in photo, has usual black visceral peritoneum. Note everted hemipenes, fat bodies just anterior to pelvis, and black visceral and abdominal peritoneum. Air sacs (a partly-filled air sac is marked by black arrow in Fig. 12B) are attached to posterior part of lungs only in *C. namaquensis*. Scale in mm.

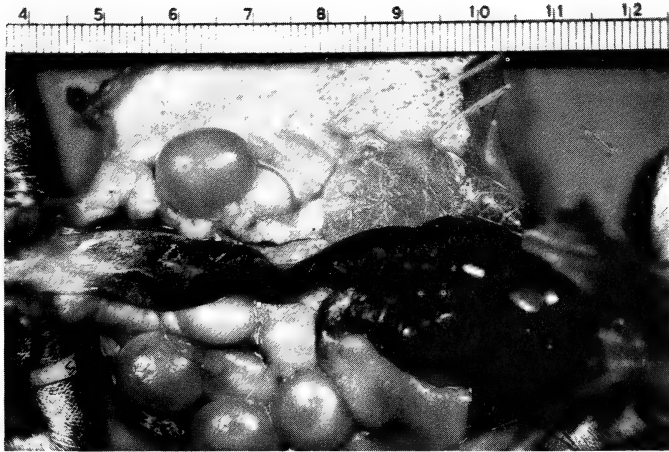


Fig. 12A.

10mm

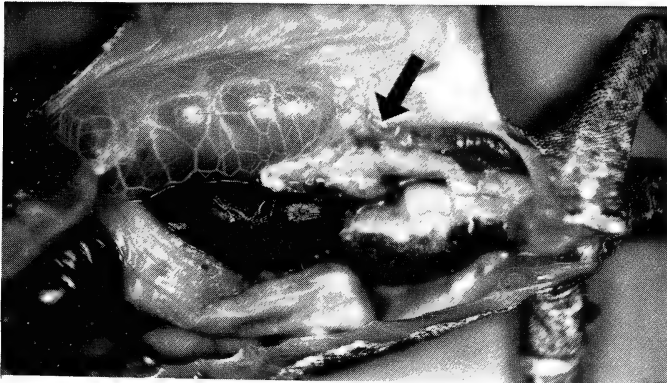


Fig. 12B.

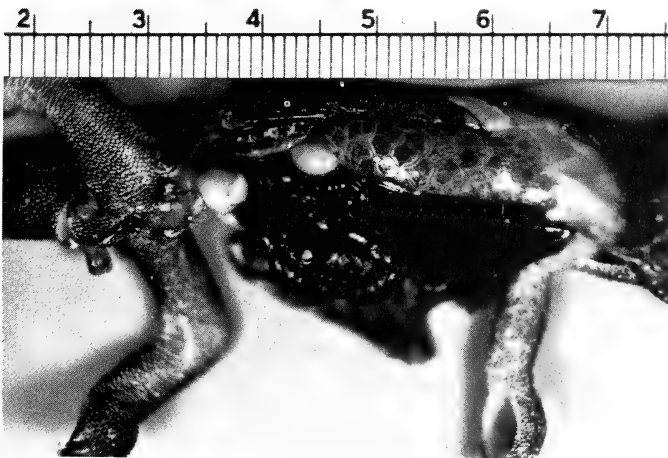


Fig. 12C.

Discussion and review of the complex reptilian reproductive cycles are given by Parkes (1956), Miller (1959), Forbes (1961) and Mayhew (1968), almost all of which deal with north temperate reptiles and virtually no complete information is given on chamaeleons. Bons & Bons (1960) found the Mediterranean *Chamaeleo chamaeleon* mates in August or September and lays eggs in October and November, which is the tropic cycle with egg-laying during or at the end of the rainy season, and not of the Mediterranean, with egg-laying at the end of spring. Bourgat (1968b) found *C. pardalis* of Réunion does not have spermatogenesis during July and August (winter). The East African *C. dilepis* lays its eggs in March (Wager 1958), September, just after the rainy season (Milner 1949), late summer (FitzSimons 1943), February (Cott 1934) and February to April (Brain 1961). Of West African chamaeleons, *C. gracilis* lays its eggs in September at the end of the rainy season (Menzies 1958), while *C. basiliscus* lays its eggs in December in captivity (Shaw 1960). *C. chamaeleon zeylanicus* of India lays its eggs in November (Trench 1912).

Ovarian cycles of reptiles are of several types, which are not yet possible to correlate to taxonomic, geographic, or climatic differences: (1) much yolk is deposited shortly prior to ovulation, but subsequent to a long slow initial growth of the ova; (2) yolk deposition occurs gradually through most of the year preceding ovulation; (3) yolk deposition occurs shortly after ovulation and mature ova occur in the ovary through the winter; (4) two sets of ova are produced and ovulated per year, each set being formed directly after ovulation of its predecessor; (5) non-seasonal breeders, producing at any time of the year. The mediating effects of the male cycle have been alluded to and presumably also act on the female cycle. For example, Tinkle & Irwin (1965) found *Uta* females to be stimulated by warmth, as did Marion (1970) for female *Sceloporus undulatus*.

10. Gestation

The corpora lutea of *Chamaeleo pumilus* appear as yellowish-white, imperfect doughnut-shaped structures as large as 4×2 mm in females that have recently ovulated, maintaining a diameter of 2 mm throughout pregnancy. Corpora lutea of the previous litter were distinct at 1.8 mm diameter, but whitish, for some time during the term of the next successive litter. Gestation in *C. pumilus* was as short as 60 days in the case of litters conceived in March and born in May, when subjected to the hottest environmental temperatures, but at other times gestation was as long as approximately 90 days. The overall ($N = 56$), average gestation period was 72 days. Those conceived in April and May and born in September did not begin oviducal development until mid-June, or the latter part of July. Three months is the approximate gestatory period for all reported viviparous chamaeleons, *C. pumilus* (Atsatt 1953; Wager 1958; Von Frisch 1962; Bustard 1963; Spence 1966; Busack & Busack 1967), *C. bitaeniatus* (Bustard 1966) and *C. hohnelii* (Bustard 1965). This study cannot agree with Rose's (1950) casual observation that gestation in *C. pumilus* is, '... well over a year'.

Pregnant *C. pumilus* nearly always maintained a Colour Index of '5', and, as such, were most conspicuous in their habitat and by their habits, being abroad in inclement weather, long after the males and non-pregnant females had sought shelter in the depths of the bushes. This greater activity of pregnant females made them seem the predominant sex. Bourgat (1968a) notes that gravid *C. pardalis* are the most active individuals. Continually basking pregnant females improve development of their winter-borne young. The dermal melanin deposit, the black abdominal, and uterine visceral peritoneum protect the young from the intense insolation they were subjected to. Pregnant females in warm months basked far less frequently, sought shade, and were lighter. Young were quite harmed by excessive heat. In laboratory tests 5 pregnant females that were subjected to temperatures above 35 C gave birth, usually prematurely, to 56 young, of which 20% had malformations of the eyes and/or head, 1% were club-tailed, and 10% were still-born.

Developing oviducal eggs (*Chamaeleo namaquensis*) and embryos (*C. pumilus*) are arranged longitudinally in the oviducts on either side of the mid-line. As they develop, the eggs (*C. namaquensis*) and embryos (*C. pumilus*) take up more and more space until they almost fill the posterior part of the coelom, but unlike many other lizards the viscera are not crowded anterior of their normal position, rather they are forced ventrally. The developing oviducal eggs (*C. namaquensis*) and embryos (*C. pumilus*) are offset, so that the egg or embryo in the contralateral oviduct more or less fits between two eggs or embryos in the ipsilateral oviduct, with the viscera forced ventrally. Such an arrangement allows both species to continue their voracious feeding in maintenance of their high metabolic rates. *C. pumilus* fed until a few days prior to birth; *C. namaquensis* never stopped.

In *C. namaquensis* the corpora lutea are about 2 mm in diameter and held at that for the entire gestatory period of 35–45 days. They regress rapidly after oviposition, though some were recognizable at the time of ovulation of the next successive clutch. In those five *C. pumilus* that had corpora lutea excised, there was no effect on litter development of foetuses that had passed pholidosis. But in those with less mature embryos, these young were resorbed. In the four gravid *C. namaquensis* excision of corpora lutea did not affect those eggs near oviposition, but resorption resulted of eggs recently ovulated. *C. namaquensis* eggs are ovulated at sizes of 13 mm or greater in diameter, and are very large at oviposition showing a clearly marked embryonic development. Compared to the eggs of other oviparous chamaeleons so far examined, the highly advanced states of development of recently oviposited eggs of *C. namaquensis* may indicate that this species is developing ovoviviparity.

The oviducts of *Chamaeleo pumilus* have distinct incubatory chambers (Figs 13, 14), each of which is supplied from a single large artery and drained by a prominent vein running dorsally along the surface of the oviduct in mid-line. These chambers are similar to those described by Weekes (1935) and Kasturirangan (1951). *C. pumilus* oviducts maintain their shape even between

Fig. 13.

A. Excised oviduct of *Chamaeleo pumilus* showing 10 full-term fetuses near birth, their yolk supplies exhausted, and one egg being resorbed, which has been excised from the oviduct and is in centre of photo. In excised ovaries (just to left of egg being resorbed) note 10 corpora lutea for full-term fetuses in upper ovary, which matches this oviduct. The egg being resorbed has long since lost its corpus luteum.

B. Incubatory chambers of an excised *C. pumilus* oviduct (anterior at top of photo). Incubatory chamber at top has had an egg (embryo and yolk sac at top) removed to show vascular supply of chamber. Egg at bottom of photo has had egg membrane peeled off, which is shown immediately to the right to show foetal vascular supply. Note, at extreme right of photo, egg not in a defined incubatory chamber, undergoing resorption. Scale in mm.

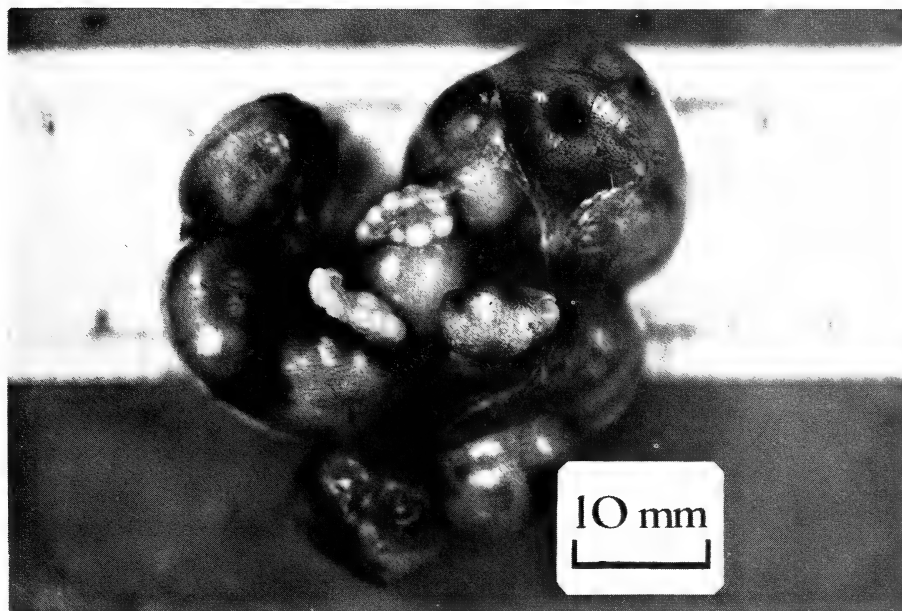


Fig. 13A.

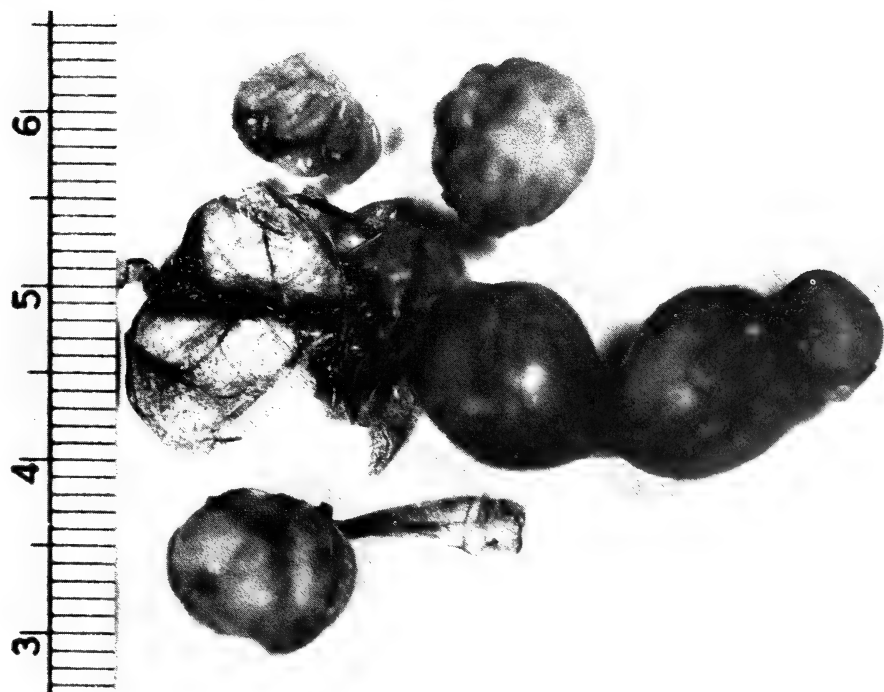


Fig. 13B.

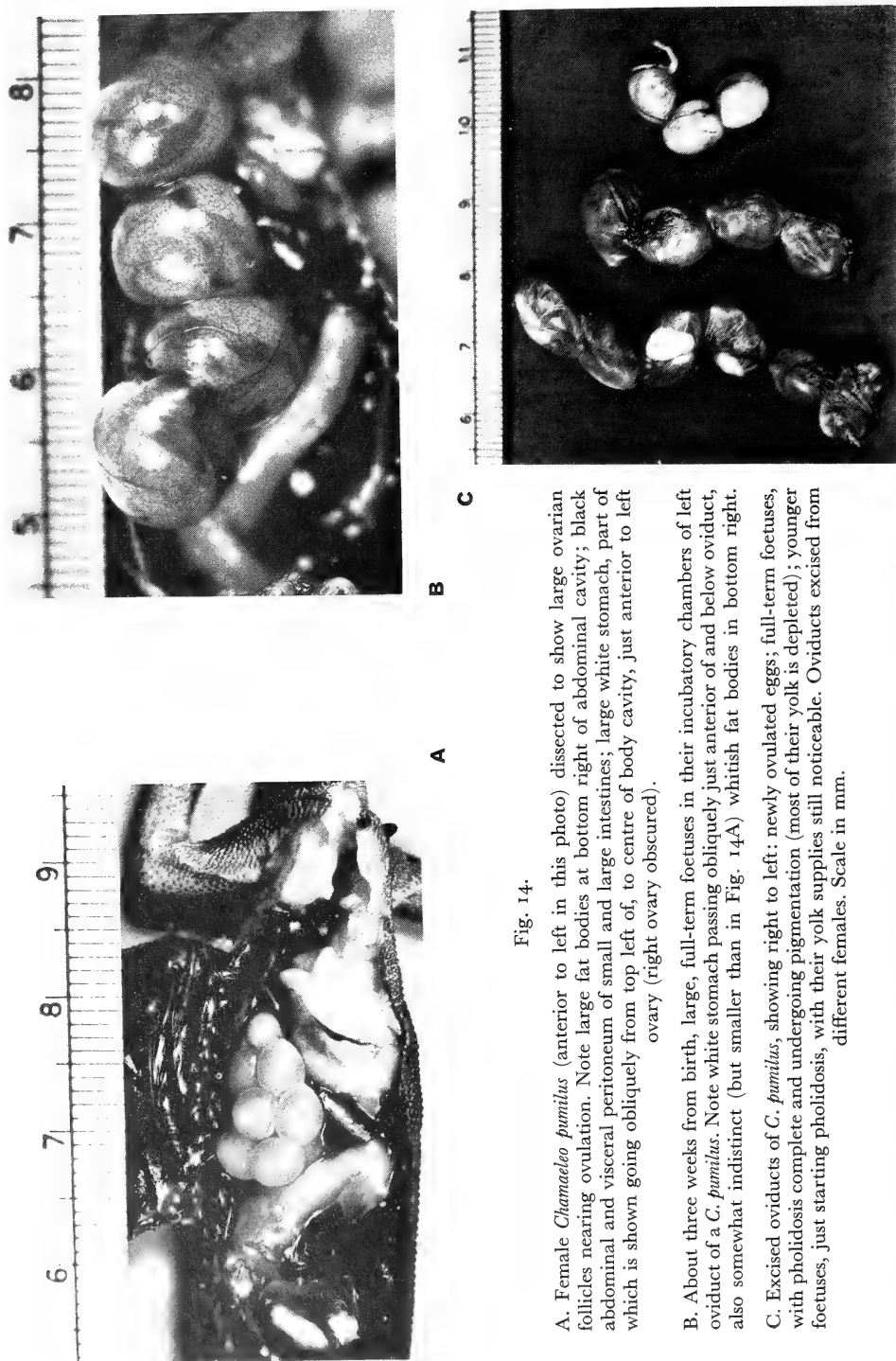


Fig. 14.

- A. Female *Chamaleleo pumilus* (anterior to left in this photo) dissected to show large ovarian follicles nearing ovulation. Note large fat bodies at bottom right of abdominal cavity; black abdominal and visceral peritoneum of small and large intestines; large white stomach, part of which is shown going obliquely from top left of, to centre of body cavity, just anterior to left ovary (right ovary obscured).
- B. About three weeks from birth, large, full-term foetuses in their incubatory chambers of left oviduct of a *C. pumilus*. Note white stomach passing obliquely just anterior of and below oviduct, also somewhat indistinct (but smaller than in Fig. 14A) whitish fat bodies in bottom right.
- C. Excised oviducts of *C. pumilus*, showing right to left: newly ovulated eggs; full-term foetuses, with pholidosis complete and undergoing pigmentation (most of their yolk is depleted); younger foetuses, just starting pholidosis, with their yolk supplies still noticeable. Oviducts excised from different females. Scale in mm.

pregnancies and the chambers are distinct, crumpled areas. The placentae of *C. pumilus* are best assigned to Weekes' Type 'I', since the yolk content of the eggs is not markedly reduced at ovulation. Recently ovulated eggs (7.0–8.0 × 6.0–6.5 mm) often have a developing embryonic area of 2–4 mm diameter. In *C. pumilus* the yolk sac placentae eventually gives way to an allanto-placentae, and most young about two weeks from birth have empty yolk sacs. Good reviews of viviparous adaptations in other reptiles and the maternal-foetal relationship are those of Boyd (1942), Cate-Hoedemaker (1933), Flynn (1923), Hoffman (1970), Wislocki (1920) and Mossman (1937). Reptiles show all gradations from the simplest maternal-foetal relationship to conditions little removed from that in eutherian mammals.

The occurrence of two closely spaced births, or two markedly different foetal age groups within the same oviducts of *C. hohnelii* (Parker 1940), *C. pumilus* (Atsatt 1953; Busack & Busack 1967) and *C. bitaeniatus* (Bustard 1966) has been attributed to secondary fertilization via sperm storage, or superfoetation, that is, two pregnancies from one mating. In these observations two closely-spaced births occurred in the September litters. Bustard (1966) thinks none of the suggested interpretations is wholly valid, as some of Parker's material is explained as atretic eggs which are being resorbed. Parker thought that such occurrences indicated all is not well. Ectopic embryos were observed in *C. pumilus*, one of which was a 'lithopedion', well-advanced and with partial adult type coloration. It was affixed to the fat body.

Since pregnant female chamaeleons resist mating, any subsequent fertilization would be most likely from sperm storage. *C. pumilus* eggs being resorbed were all ones that were not in incubation chambers, nor were full-term corpora lutea present for them, only atretic corpora lutea at best. This indicates that on some occasions, viviparous chamaeleons ovulate more eggs than there are gestation sites for. Such eggs would face resorption, and the data showed this to be so. In September, *C. pumilus* had two litters of very small size (no more than 8 young in each) that were probably conceived via sperm storage by direct mating in April and May. They were probably small, because they developed over winter in the female, on whom they must have been a considerable drain during this inclement season. Both were ovulated in mid-June or the latter part of July, apart from each other, the second litter being potential and held in the ovary at a follicular size of greater than 5 mm diameter. However, triggered by oviducal site availability, the female's physiological state, and/or other conditions favouring the development of a larger first of the year litter size, a second small September litter proceeded (ovulated) to oviducal development. The relationship of the difference of follicle sizes and developing embryos is shown in Tables 37 and 42. The September litters had the least variation in complement of any litter. The time of parturition between these two differently conceived litters was no more than two days in marked females in the field. Some captives did stretch parturition over a week, perhaps reflecting nutrition problems of captivity. The second September litter is best considered as

superfoetation, conceived at and beginning oviducal development at a closely spaced but later time from the first September litter. Both September litters were essentially born at the same time and have been treated as single litters (Table 38). The single small litters born in May were conceived by direct mating in February and March and represented a means of achieving a litter at the warmest time of the year. This allowed for recovery of the reserves of the female before development of the September litter.

Chamaeleo namaquensis eggs grew from the ovulatory size of 13 mm or greater in diameter to a mean of $20,5 \times 11,6$ mm; 1,5 g (max $26,0 \times 14,5$ mm; 2,8 g) in 25–30 days (warm season), 35–45 days (cool season) at the time they were oviposited. A small, reddish embryonic area 2 mm diameter was visible in a few recently ovulated eggs, and at the time of oviposition this area was as great as 10 mm. The oviducts of *C. namaquensis* contained distinct 'gestatory' chambers, each of which housed an egg. The vascular supply to such chambers was, however, less distinct than that of the incubatory chambers of the viviparous forms.

Brain (1961) gives a 120-day gestation period for *C. dilepis*. The gestation period of *C. namaquensis* is closest to *C. chamaeleon zeylanicus* (Trench 1912) and *C. chamaeleon* (Bons & Bons 1960) of reported oviparous chamaeleons, and to some iguanids (Burrage 1966).

11. Incubation

The overall incubation increment of *C. namaquensis* eggs was: length: 14–40% ($\bar{x} = 19,8\%$); width: 4–16% ($\bar{x} = 9,8\%$); weight: 18–65% ($\bar{x} = 37\%$). In just two days of incubation, length increased by 4–19% ($\bar{x} = 8,2\%$); width 4–9% ($\bar{x} = 6,0\%$); weight 12–40% ($\bar{x} = 27,3\%$). Increments after 60 incubatory days were slight and essentially as for the entire period. During the later stages of incubation, the large, black developing *C. namaquensis* embryo was clearly discerned through the shell. Increments for the first two and 60 incubation days were less in those clutches laid in May through July, which had the longest incubation period (May, 112; June, 100; July, 97 days). Eggs laid in early August took 91 days, as did those laid in October and September, and those of late August took 92 days. The overall ($N = 250$) incubation time was 98,4 days.

The following data are available in the literature on incubation times of chamaeleon eggs: *Chamaeleo dilepis*: 90 days (FitzSimons 1943), 219–365 days (Milner 1949; Wager 1958; Brain 1961); *C. gracilis*: 210 days (Menzie's 1958); *C. basiliscus*: 179 days (Shaw 1960); *C. chamaeleon*: 280 days (Haas 1947), and 250–260 days (Bons & Bons 1960). It was accounted by people at Cape Cross South West Africa, that *C. namaquensis* eggs laid there took twelve months to hatch. However, this is thought to have been multiple usage by several females of the same nest site, with different hatching times of the several clutches laid at various dates. Or, conversely, different clutches laid at different dates by one, perhaps two females. On the average, chamaeleon eggs take longer to

hatch than those of other saurians, but about the same time as the Australian deserticolous agamid *Moloch horridus* (56 days, White 1948; 90–132 days, Sporn 1965). Many of these chamaeleon incubation times are based on captive records, under different conditions, clutches at different times of the year, and for clutches laid by females of widely separated geographic populations.

The effect of temperature on incubating saurian eggs has been discussed in several papers, with the expected observation that longer incubation obtains at cooler times of the year. Cooper (1965) experimentally incubated clutches of lacertid eggs at different temperatures, finding maximum incubation time (122–160 days) accrued when the eggs were subject to temperature variation (18.5–21.0 °C by day; 12.5 °C by night), and least (46 days) when the eggs were incubated at a uniform 27 °C. Great disparity has been recorded in the incubation time of the eggs in natural nests of the American scincid *Eumeces fasciatus*, Fitch (1954) giving 27–47 days, and Cagle (1940) nine days. Undoubtedly, as Fitch (1954) asserts, temperature is important, but it may not be the only factor. Burrage (1966) discusses the influence of different thermal gradients of various substrates on incubation times of the eggs of *Uta*, noting that site selection at oviposition is also important, since some substrates are more favourable throughout the year. Bons & Bons (1960) have shown that chamaeleon eggs do not hatch quicker when maintained at higher temperatures (27–28 °C), but gross cephalic deformities result. Table 45 shows the temperatures of dune sand and gravel for inland and coastal sites at the 200–250 mm depth where *Chamaeleo namaquensis* laid its eggs. There was some difference in sand and gravel temperatures, but markedly higher inland substrate temperatures occurred especially in June and July, when fog was the rule at coastal sites. The greater prevalence of fog and the moderating effect of the Benguela Current depressed coastal air and surface substrate temperatures. The surface substrate maximum temperature, occurring at approximately 14:00 hours, was only reflected the following day at a depth of 200–250 mm. No oviducal eggs were found November to March (Tables 39, 44), which might be because the temperature at the

Table 45

Twenty-four hour substrate temperature (in °C) records at 200–250 mm depth for dune sand and gravel at coastal and inland locations.

Means are in parentheses.

Month	Coastal		Inland	
	Dune sand	Gravel	Dune sand	Gravel
1969				
April	23.5–28.5 (26.5)	23.0–28.0 (25.5)	27.0–35.5 (31.5)	25.0–31.0 (28.5)
June	15.0–20.0 (17.5)	14.0–21.0 (17.3)	21.0–30.0 (26.0)	20.0–33.5 (24.5)
November	22.0–31.0 (25.5)	21.0–33.0 (25.0)	26.0–33.0 (29.5)	27.5–34.0 (31.0)
1970				
February	27.0–35.0 (30.3)	25.0–33.0 (28.6)	32.0–39.0 (35.5)	31.0–39.0 (34.0)

laying depth was too high from February to April. At this time all the young had hatched and in the May clutch development proceeded only in late April as cooler temperatures returned at the laying depth. Regardless, *C. namaquensis* eggs incubated at temperatures above the 27–28 C 'harm' limit of Bons & Bons (1960), indicative of adjustment to their environment.

12. Young

Birth size data for *Chamaeleo pumilus* are given in Tables 38 and 47. The young for most litters averaged a snout-vent length of about 22 mm—the tail usually equal to or slightly less than this, and rarely in excess, regardless of sex—and a weight of 0,3–0,4 g. The smallest young (snout-vent \bar{x} = 20 mm) were those born in September, perhaps reflecting the effects of superfoetation, and the largest young (max snout-vent 27 mm; \bar{x} = 25 mm) were born in November. Males were slightly smaller than females. Table 46 gives the sex and pattern types of newborn *C. pumilus*. Recently born viviparous chamaeleons resemble the adults, except in colour and pattern, though some (Table 46), mostly males, had a true adult pattern. Brown individuals at birth were mostly females, and did not acquire the adult colour at maturity. The disparity in pattern between the young and adult of viviparous chamaeleons is noted for *C. pumilus* by Abel (1931), Von Frisch (1962) and Bustard (1963); *C. bitaeniatus* (Bustard 1966); and *C. hohnelii* (Angel 1933; Bustard 1965). The sex ratio at birth in *C. pumilus* was nearly equal. Von Frisch (1962) thinks that the newly born young of *C. pumilus* have to 'learn' to aim their tongues, but Bustard (1966) does not agree, with which this study concurs. However, it was observed that slightly premature young aimed poorly at first, but improvement of their aim is probably due to maturation of their senses, rather than 'learning'.

Table 46

Sex and pattern types at birth of 614 *Chamaeleo pumilus* expressed as percentages. The number not enclosed in parentheses shows the percentage of a given sex having a particular pattern type, while the number enclosed in parentheses shows the percentage of that sex of that particular pattern type in the total sample.

Sexes		Pattern types							
Male	Female	Adult		Gray-green		Gray		Brown	
38–64	36–62	Male	Female	Male	Female	Male	Female	Male	Female
\bar{x} = 51	\bar{x} = 49	50,0 (20,0)	16,5 (10,0)	25,0 (10,0)	26,4 (16,0)	15,0 (6,0)	23,1 (14,0)	10,0 (4,0)	34,0 (20,0)

Data on *Chamaeleo namaquensis* oviposition and hatching dates and the time to reach maturity are given in Table 49. Recently hatched male *C. namaquensis* varied in total length from 45,0–55,0 mm (20,0–25,0+25,0–30,0 mm); means: total length: 50,0 mm; snout-vent: 22,5 mm; tail: 27,5 mm; and all weighed about 0,6 g. Females were larger, varying in total length from 55,0–65,0 mm (30,0–35,0+25,0–30,0 mm); means: total length: 60,0 mm; snout-vent: 32,5 mm; tail: 27,5 mm; and weighed 1,0–1,7 g (\bar{x} = 1,5 g). The young were

mere miniatures of the adults as to pattern and colour, but possessed more vertebral knobs (see also FitzSimons 1943). *C. dilepis* (Brain 1961) and *C. basiliscus* (Shaw 1960) hatchlings are also miniatures of their adults. *C. namaquensis* young hatched out late in the evening and during the night, and rapidly dispersed. Unlike the adults, they preferred to climb and could be found on grass stems and other vegetation, or perched on rocks. (A February hatchling, photographed in early March, is shown in Figure 11.)

13. Growth and longevity

The growth of young *Chamaeleo pumilus* is shown in Table 47. As time passed, the size differences narrowed between the various litters. Data on juvenile *C. pumilus* fat body weights, gonadal sizes and weights are given in Table 48. In *C. pumilus* and *C. namaquensis* juvenile testes were flattish with thin, whitish epithelium, and loosely convoluted tubules; the sperm ducts were flat and thin, whitish opaque, straight to wavy. In females the oviducts were collapsed and thin, black in *C. pumilus*, and silvery in *C. namaquensis*. The ovaries were longer than they were wide and somewhat transparent, bearing follicles no larger than 1.5 mm diameter. Upon hatching and at birth, follicle size was not more than 0.25 mm, and the entire ovaries were about 2.0×1.0 mm. The testes were about 1.0×0.75 mm and translucent.

Table 47

Mean growth rates to maturity of 148 *Chamaeleo pumilus* in the field. Both sexes mature at a snout-vent length of 50 mm. Roman numerals represent months.

Birth date	Mean snout-vent (mm) at birth	Mature date (days)
II	22.0	210
III	22.0	240
IV	22.0	240
V	22.0	240
IX	20.0	169
XI	25.0	85
XII	22.0	108

Busack & Busack (1967) give data on the growth of a November brood of 12 *Microsaura pumila* (= *C. pumilus*) over 300 days, some of which present different growth curves. One of Busack & Busack's young chamaeleons reached 60 mm (snout-vent) in 175 days, another measured 37 mm (s-v), and one 43 mm (s-v) in 135 days. One chamaeleon reached 60 mm (s-v) in 262 days, and another did not grow in 143 days from 20 mm (s-v) at birth. Half of Busack & Busack's sample did not live over 50 days. Bustard (1965) records a male *Chamaeleo hohnelii* that increased in 18 days from a total length of 95 to 110 mm, acquiring sexual maturity, though he is not sure of its exact age.

Table 48

Juvenile male and female *Chamaeleo pumilus* and *C. namaquensis* showing fat body weights, testes weights and dimensions, weights and dimensions of ovaries and ovarian follicle size. Sizes are in millimetres; weights in grams. Means are in parentheses.

	Testes		
	Fat body weight	Weight	Size
Males			
<i>C. pumilus</i>	0,001-0,015 (0,006)	1,0-3,5 × 0,8-2,0 (2,1 × 1,3)
<i>C. namaquensis</i>	0,001-0,003 (0,002)	2,5-3,0 × 1,5-2,0 (2,7 × 1,8)
Size of 24 juvenile <i>C. pumilus</i> examined: body weight 0,3-1,4 g \bar{x} = 0,8; snout-vent 27,5-46,0 mm \bar{x} = 34,9; tail 25,0-44,0 mm \bar{x} = 34,7.			
Size of 7 juvenile <i>C. namaquensis</i> examined: body weight 3,0-7,0 g \bar{x} = 4,0; snout-vent 40,0-46,0 mm \bar{x} = 42,0; tail 30,0-37,0 mm \bar{x} = 33,5.			
	Ovary		Follicle size
	Fat body weight	Weight	Size
Females			
<i>C. pumilus</i>	0,001-0,080 (0,040)	1,0-4,0 × 0,5-3,0 (2,5 × 1,5)
<i>C. namaquensis</i>	0,001-0,091 (0,071)	1,3-4,1 × 0,7-3,2 (3,4 × 1,9)
Size of 32 juvenile <i>C. pumilus</i> examined: body weight 0,4-2,5 g \bar{x} = 1,0; snout-vent 24,0-51,0 mm \bar{x} = 31,2; tail 23,0-51,0 mm \bar{x} = 31,5.			0,5-1,5 (0,7)
Size of 6 juvenile <i>C. namaquensis</i> examined: body weight 3,0-4,0 g \bar{x} = 3,8; snout-vent 30,0-37,0 mm \bar{x} = 33,0; tail 29,0-33,0 mm \bar{x} = 32,0.			0,5-1,5 (0,7)

C. pumilus and *C. namaquensis* in the field grew faster and less erratically than those in captivity. A captive *C. pumilus* grew faster than those viviparous chamaeleons reported in the literature, but some registered the same sort of erratic growth and there were runts, who grew little or not at all. Also, most literature references do not record the sex of the young.

Table 49 shows growth rates for *C. namaquensis* young from hatching to maturity. Females reached maturity in 150 days at a snout-vent length of 75–80 mm. Males reached maturity in 210 days at a snout-vent length of 70–75 mm. Table 48 shows fat body weights, gonadal sizes and weights of juvenile *C. pumilus* and *C. namaquensis*. Growth was steadier and faster in female *C. namaquensis*; while the overall male growth rate was slower it was faster over the first and last 30 day periods (3 mm per diem). Juvenile *C. namaquensis* preferred climbing and were far more adept at this than adults. Their thermoregulatory pattern was adult in every respect. As they neared maturity, their increased stockiness and larger size made for injurious falls, when they tried climbing the same structures that easily supported them at a smaller size.

Table 49

Mean growth rates to maturity of 107+ *Chamaeleo namaquensis*, mostly in the field. Males matured in 210 days at a snout-vent length of 70–75 mm; females matured in 150 days at a snout-vent length of 75–80 mm.

Month eggs laid	Incubation period (in days)	Sex	Number of days for young to reach maturity
May–July	97–112	♂♂	210
		♀♀	150
August	91	♂♂	210
		♀♀	150
August–September	91–92	♂♂	210
		♀♀	150
October	91	♂♂	210
		♀♀	150

Considerable differences have been reported for the growth of oviparous chamaeleons. Brain (1961) feels that *C. dilepis* takes a long time to acquire maturity, citing a two-year-old that was still juvenile and sexually immature. However, Wager (1958) notes a *C. dilepis*, 45 mm long at hatching, had reached 152 mm seven months later. After seven months the growth of this individual slowed, and at 13 months its total length was 216 mm, having gained only 63 mm in the final six months of observation. Wager thinks *C. dilepis* matures in a year. The growth rate of chamaeleons does not seem unusually slow or fast in comparison with that of other saurians recorded in the literature (Mayhew 1968) and the influence of hatching times of different clutches of different species and populations undoubtedly varies, as the geographic and climatic conditions obtaining in the respective areas each inhabits. Menzies (1958) reports that *C. gracilis* hatch at the onset of the rainy season, which

might be inclement enough to retard growth. *C. namaquensis* was little affected by rainy seasons, and all young hatched out after the fogs of June and July. Furthermore, food in the Namib Desert was always abundant and young and old chamaeleons gorged to the limit; a condition not often enjoyed by captives, whose feeding by their captors is an exhausting task (see also Abel 1931 and Bustard 1963). As Bustard (1963) observes, captive chamaeleons are at a liability, the limits of captivity showing the mere minimum they are capable of.

There is no good knowledge of the life-span of chamaeleons, though Brain (1961) feels that *C. dilepis* reaches 10–20 years, and hearsay puts *C. pumilus* at a maximum of six years. Three years of study on marked *C. pumilus*, showed amazing longevity of individuals in the field, some 40% of the adults, plus some progeny recorded and marked in February, 1969, being recovered in February, 1971. *C. namaquensis* was not observed over a long enough period—though recovery was quite high—but, as with *C. pumilus*, and as Bourgat (1968a) observed for *C. pardalis*, there was tremendous fluctuation according to the season. At the end of a year he recovered 60 of 140 he had marked.

IV. SUMMARY.

Various aspects of the life histories of the chamaeleonids *Chamaeleo pumilus* (Gmelin) and *C. namaquensis* A. Smith were investigated in the field and laboratory from 13 January 1969 to 30 November 1970 in the Republic of South Africa and South West Africa. A total of 494 *C. pumilus* and 207 *C. namaquensis* were marked for field studies by branding or leg bands. *C. pumilus* inhabit any vegetation guaranteeing a plentiful source of prey. They were studied at Port Nolloth, Leeu-Gamka, Beaufort West, Van der Stel station, The Strand and chiefly at Stellenbosch. While primarily of arboreal habits, *C. pumilus* frequently walks along the ground, such ground-dwelling habits being especially true of those inhabiting arid and semi-arid areas. *C. namaquensis* is ubiquitous in desert and near desert areas. Adults are exclusively ground-dwelling, even invading the desert littoral intertidal zones. *C. namaquensis* was observed in South West Africa at Gobabeb, Tsondab, Geluk Farm, Solitaire, Rehoboth, and on the coast from Walvis Bay north to Cape Cross.

The only recorded instance of ectoparasites were *Culex* mosquitoes feeding on *C. namaquensis* at Gobabeb. There was some seasonal and sexual variation in the incidence and degree of endoparasitism in *C. pumilus*, the females harbouring more parasites than the males. The nematode *Strongyluris* was the principal intestinal helminth of *C. pumilus*. The cestode *Oochoristica africana* was the principal intestinal helminth of *C. namaquensis*. Cysts and larval worms occurred in both chamaeleons. Snakes and birds were the principal predators on *C. pumilus*. Raptorial birds were the chief predators on *C. namaquensis*. Physical factors and human activities also affect chamaeleons.

The body temperatures of 549 *C. pumilus* active in the field ranged from 3.5 C to 37.0 C (mean 22.4 C; median 22.8 C). The body temperatures of

351 *C. namaquensis* active in the field ranged from 14,0 C to 39,7 C (mean 28,7 C; median 28,8 C). In laboratory preferred body temperature gradients, 20 *C. pumilus* were active from 7,0 C to 30,0 C (mean 25,0 C) and 18 *C. namaquensis* were active from 18,5 C to 36,2 C (mean 29,3 C). While body temperatures of *C. pumilus* varied according to the weather and season, those of *C. namaquensis* were much more stable, though the body temperatures of inland and coastal populations differed slightly. Field records of nocturnal body temperatures of both species at rest were close to the environmental temperature, while those in captivity were slightly higher.

Chamaeleons regulate their body temperatures by a complexly integrated physiological process, involving dermal colour lability with attendant vasomotor and other cardiovascular adjustments, body posturing, thermo-pneumatic changes in the volumes of the lungs and air sacs, and panting. The role of dermal colour lability was examined in laboratory experiments using 30 *Chamaeleo pumilus* and 28 *C. namaquensis*. Dark-adapted chamaeleons are warming, light-adapted individuals are cooling. By changing the body contour by compression and posturing, chamaeleons regulate the heat and light load striking their bodies. At any given temperature, the heart rates of 5 each of *C. pumilus* and *C. namaquensis* were higher during heating than cooling. Live chamaeleons heated faster than they cooled, whereas dead ones heated and cooled at the same rate.

The peak oxygen consumption in 15 *C. pumilus* was at 25 C, while the greatest active Q_{10} (1,29) value was over the 5–15 C range. The peak oxygen consumption of 15 *C. namaquensis* was at 35 C, while the greatest active Q_{10} (2,91) value was over the 25–35 C range.

C. pumilus and *C. namaquensis* were active throughout the season under all weather conditions, and were active from about sunrise to sunset, except ovipositing *C. namaquensis* were active throughout the night. Many newly hatched *C. namaquensis* came out during the night.

Partially blinded chamaeleons either naturally or experimentally developed an accuracy of 57,0–63,0% (\bar{x} = 60,0%) in catching prey, whereas the accuracy of normal *C. pumilus* was 75,0–92,0% (\bar{x} = 86,0%) and that of *C. namaquensis* was 80,0–90,0% (\bar{x} = 85,0%).

In *C. pumilus* the tongue can pull a weight equal to two-thirds or one-half of the body weight and be maximally projected to a length about two-thirds of the total length of the animal. In *C. namaquensis* the tongue can pull a weight equal to the body weight of the individual chamaeleon and be maximally projected to a length equivalent to that of the snout-vent of the animal. The prey is held by a mechanical overlapping of the bi-lobed tongue knob at the tip of the tongue.

By selecting prey of certain sizes, both chamaeleons could realize a greater intake of food than by eating very large prey items. *C. pumilus* realized maximal ingested volumes by selecting muscid flies, its principal prey, and small tenebrionid beetles. *C. namaquensis* realized its greatest daily volumes of food when

meals were composed of small locustids and large tenebrionids. *C. namaquensis* took about 19 or 23 large tenebrionids per meal, with a minimum of 5 to a maximum of 15 ($\bar{x} = 12$) daily meals. *C. pumilus* and *C. namaquensis* were voracious feeders and rapidly food. Two to five hours were required to digest and eliminate meals taken in during the day and up to 12 hours for meals taken before retirement and digested overnight.

In *Chamaeleo pumilus* (♂♂64; ♀♀86) there were seasonal and apparently sexual variations in diet. Dipterans were the main prey item, but the families selected varied with the sex of the chamaeleons. At some times of the year the prey eaten by the females, for example, was either not the same as that eaten by the males, or the proportions taken varied tremendously. Inland (N = 64) and coastal (N = 157) *C. namaquensis* preyed mostly on large tenebrionids. Plant and inorganic matter were also ingested. Mammal hair and bird feathers occurred in inland samples, and reptiles were taken by coastal *C. namaquensis*. Strand-dwelling *C. namaquensis* fed on flies, intertidal arthropods, tenebrionids, and reptiles.

Water is of crucial importance to chamaeleons, and they cannot survive on food alone. Desiccation experiments were run on 18 each of *C. pumilus* and *C. namaquensis*. In one test they were given food but no water for 12 days and then food and water for 3 additional days. In a second test they were without food and water for 7 days. In both experimental sets, the haematocrit values of dehydrated *C. pumilus* were 28,6–33,7 ($\bar{x} = 31,3$) and plasma osmolality values 395,0–440,0 mOsm ($\bar{x} = 421,3$), and the haematocrit values of dehydrated *C. namaquensis* were 14,6–19,8 ($\bar{x} = 17,6$) and the plasma osmolality values 230,0–255,0 mOsm ($\bar{x} = 246,3$). In rehydrated *C. pumilus* the haematocrit values were 14,5–29,0 ($\bar{x} = 21,4$) and the plasma osmolality values 200,0–210,0 mOsm ($\bar{x} = 203,8$), and the haematocrit values of rehydrated *C. namaquensis* were 15,5–32,5 ($\bar{x} = 24,6$) and the plasma osmolality values 219,0–292,0 mOsm ($\bar{x} = 261,3$). These data suggest water storage in the vascular space of both chamaeleons. Seven freshly caught *C. pumilus* had haematocrit values of 29,0–30,5 ($\bar{x} = 29,9$) and plasma osmolality values of 200,0–210,0 mOsm ($\bar{x} = 203,8$). Eight freshly caught *C. namaquensis* had haematocrit values of 42,0–50,0 ($\bar{x} = 46,6$) and plasma osmolality values of 220,0–290,0 mOsm ($\bar{x} = 259,8$).

C. namaquensis has a salt gland and samples of the exudate of this showed excretion of sodium, chloride, and potassium in the ratio of 6,4: 7,0: 1,0; respectively. While this gland undoubtedly is of value in strand-dwelling chamaeleons to excrete any salt ingested with the intertidal prey on which they feed, its chief function is probably to enable *C. namaquensis* to produce a urine of low water content by re-excreting electrolytes which have been reabsorbed in the cloaca. This would greatly benefit the water economy of those *C. namaquensis* inhabiting regions outside the fog belt.

Chamaeleo pumilus adults were most dense in December (195 individuals, 2 437,5 g per hectare), with significant secondary peaks in January (118

individuals, 1 105,0 g per hectare), and October (120 individuals, 1 116,0 g per hectare). Juveniles were most dense in February and March as components of the overall population. Of all *C. pumilus* marked in February 1969, 40% were recovered two years later. Biomass and density of adult *C. namaquensis* were relatively consistent, increases in the biomass reflecting the heavier weights of gravid females. *C. namaquensis* also had a high recovery rate.

C. pumilus and *C. namaquensis* display in a series of side-to-side head bobs. *C. pumilus* and *C. namaquensis* resort to fighting if the transgressing chamaeleon does not leave the defender's presence.

Both sexes of *C. pumilus* have an undefended, shifting, vertical home range averaging 10 m² in plan view. However, since these chamaeleons use their home ranges as if they were layered, the actual area is about 600 m². If the food sources failed, the home range locus was shifted. Only a favoured perch was defended by both sexes of this species.

C. namaquensis occupied very rigidly delimited territories. Female territories and territories limited to one biotope or habitat were the smallest. Male territories increased in area during courting and those of females enlarged during egg-laying. Juveniles occupied a small, shifting home range within the rigidly defended territories of the adults from whom they were free of challenge.

In June and July male *C. pumilus* showed total regression of the testes and in August most male *C. namaquensis* had inactive testes. Yolk deposition occurred in follicles of 2 mm diameter in adult female *C. pumilus* and *C. namaquensis*. *C. pumilus* eggs were ovulated at 7,0–8,0 × 6,0–6,5 mm and in *C. namaquensis* at a diameter of 13 mm or greater. Development of ovarian follicles is brought to and held at 4 mm diameter if oviducal development of embryos or eggs is in progress. Ovarian follicular development does not proceed until the litter developing in *C. pumilus* had at least reached pholidosis and in *C. namaquensis* until the oviducal eggs were being shelled or their laying was imminent. Recently ovulated *C. namaquensis* eggs have a reddish embryonic area of 2 mm, and at the time of oviposition this area was as great as 10 mm.

The gestation period in *C. pumilus* was as short as 60 days in the case of litters conceived in March and born in May to as long as about 90 days at other times. Gestation lasted 35–45 days in *C. namaquensis*. *C. pumilus* females about to give birth select small-leaved shrubs, and *C. namaquensis* females oviposit in burrows which they dig to a depth of 200–250 mm.

Sexually mature female *Chamaeleo pumilus* had four litters annually, the size of the female having some relation to the size of the litter. Births were recorded in February to May, September, November and December. The largest litters (5–21; \bar{x} = 17,0 young) were born in December; the smallest in April (3–6; \bar{x} = 4,5 young), for an overall range of 3–21 (\bar{x} = 11,0 young). Newly born *C. pumilus* quickly freed themselves of their membranes, and have a mean snout-vent of about 22 mm; the smallest are those born in September (snout-vent mean of 20 mm) and the largest those born in November (snout-vent mean of 25 mm). The pattern of the young differs from that of the adults.

Growth is rapid, maturity being reached in both sexes at a snout-vent of 50 mm, taking 85 days for those born in November to as much as 240 days in those born in March, April and May.

C. namaquensis had at least two to three clutches of eggs per year, and these eggs are laid from May to September. Clutches laid in September (6–13; \bar{x} = 9,5 eggs) were the smallest in complement and those laid in July (10–22; \bar{x} = 13,0 eggs) were the largest. Of 250 *C. namaquensis* eggs examined, sizes at oviposition varied from 17,5–26,0 × 10,0–14,5 mm; 1,2–2,8 g (\bar{x} = 20,5 × 11,6 mm; 1,5 g). Eggs laid in September were slightly larger than those laid at other times. When first laid, eggs were beige, becoming immaculate white with thin parchment-like shells.

Eggs laid in early August, September, and October took 91 days to hatch, while those laid in May took 112 days. The overall incubation period was 98,4 days. The length of the incubation period is apparently related to the temperatures at the depth at which the eggs were laid. The overall incubation increment of *C. namaquensis* eggs was: length 14–40% (\bar{x} = 19,8%); width 4–16% (\bar{x} = 9,8%); and weight 18–65% (\bar{x} = 37,0%).

Recently hatched male *C. namaquensis* varied in total length from 45–55 mm and all weighed about 0,6 g. Females were larger, varying in total length from 55–65 mm and weighed 1,0–1,7 g (\bar{x} = 1,5 g). They were identical to the adults in appearance, except the young had more vertebral knobs. The young have an affinity for climbing. Male *C. namaquensis* matured in 210 days at a snout-vent of 70–75 mm and females in 150 days at a snout-vent of 75–80 mm.

Excision of the fat bodies resulted in a decline of testicular activity in four males each of *C. pumilus* and *C. namaquensis*. Excision of the fat bodies in four female *C. namaquensis* retarded or prevented ovarian follicular growth in pre-estrous females. In early estrous females fat body excision induced a high incidence of follicular atresia and retarded the yolk deposition rate. In six female *Chamaeleo pumilus* fat body excision retarded or prevented ovarian follicular development, and only pregnant females with the young near birth actually completed delivery.

Corpora lutea were large and prominent in *C. pumilus* and *C. namaquensis* females during the gestation period. Excision of corpora lutea in five pregnant female *C. pumilus* had no effect on litter development of those young that had passed pholidosis, but in those females with more immature young, corpora lutea excision resulted in resorption. In four gravid female *C. namaquensis*, excision of the corpora lutea did not affect the oviposition of those eggs about to be laid, but recently ovulated eggs were resorbed. Developing oviducal embryos in *C. pumilus* and developing oviducal eggs in *C. namaquensis* apparently rest in specific chambers in the oviducts during gestation, and if insufficient sites are available in *C. pumilus*, the surplus ovulated eggs were resorbed and their corpora lutea degenerated.

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FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Etudes sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627-634.

KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309-320.

KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1-51.

THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika*. **4**: 269-270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269-270.

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CHAMAELEO PUMILUS PUMILUS (GMELIN)
AND *C. NAMAQUENSIS* A. SMITH
(SAURIA: CHAMAELEONIDAE)





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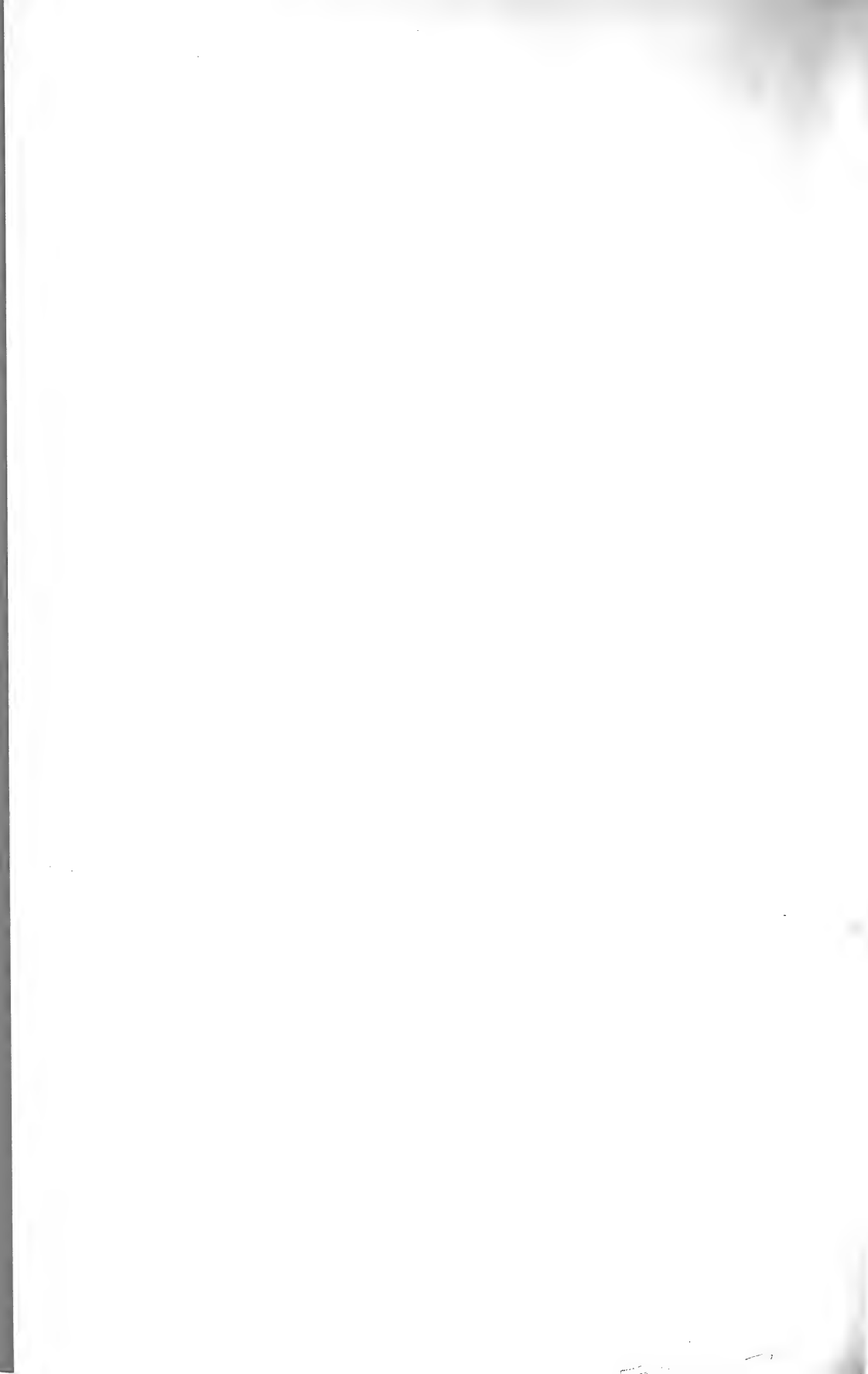
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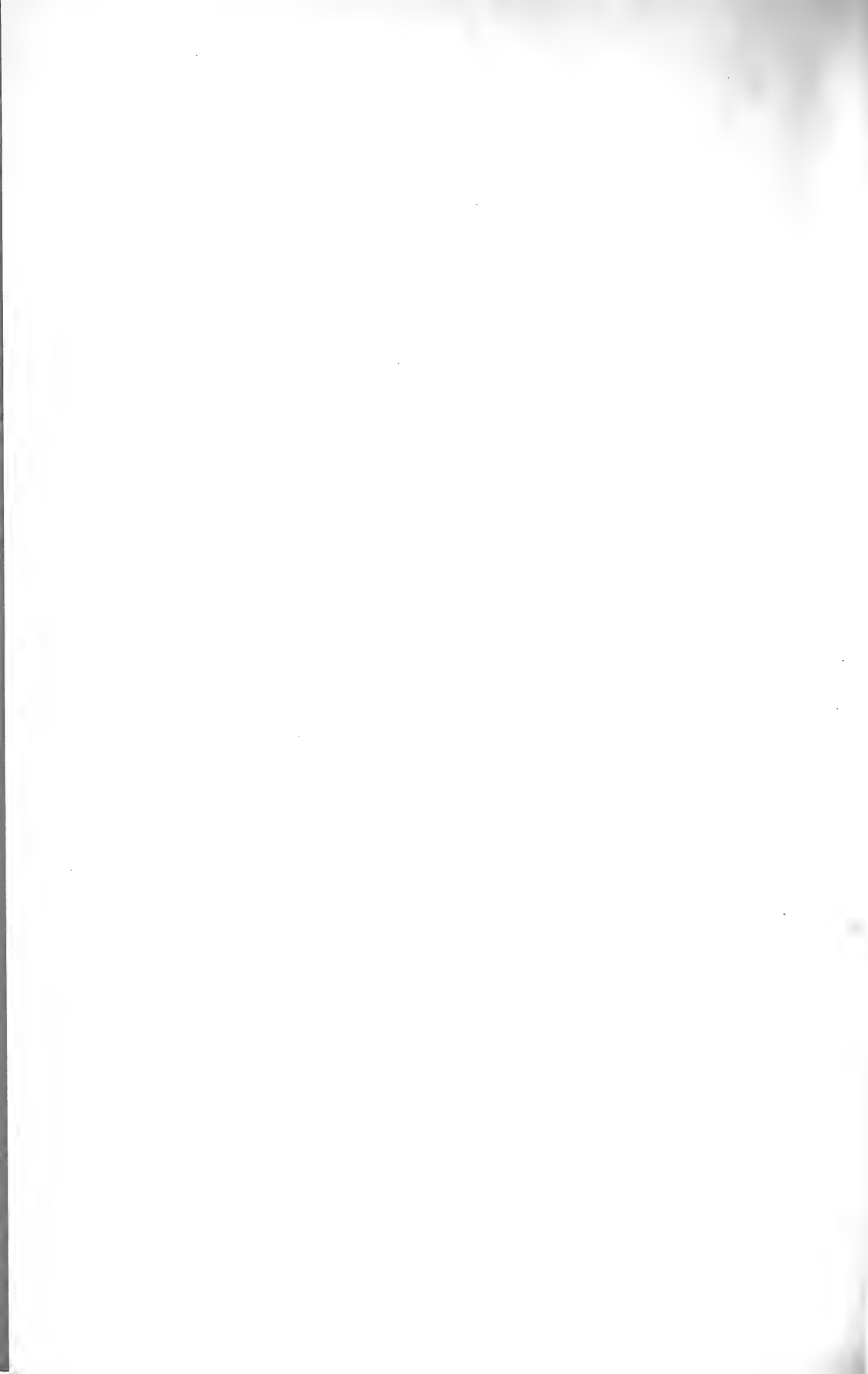


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AFRICAN FORMICIDAE (HYMENOPTERA) IN
THE SOUTH AFRICAN MUSEUM
DESCRIPTION OF FOUR NEW SPECIES AND
NOTES ON *TETRAMORIUM* MAYR

By
A. J. PRINS

Cape Town Kaapstad

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By

A. J. PRINS

South African Museum, Cape Town

(With 40 figures)

[MS. accepted 11 October 1972]

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INTRODUCTION

In view of the fact that most of the descriptions of the various types of ants of South Africa are inadequate and the drawings which are available lack any detail of the sculpture and setae, I have decided to illustrate those available to me in museums in South Africa and Rhodesia, and I hope that this will help other myrmecologists who find it almost impossible at the moment to identify the various forms. As no types or paratypes are available of *Tetramorium solidum* Emery *signata* Em. and *T. jauresi* Forel, drawings were made from specimens determined by Arnold for the purpose of clarifying their position in the proposed key.

Among the Tetramoriini, those species that belong to the *solidum* group, which have the epinotal spines as long as wide at their bases, have always been

identified with great difficulty, especially those from the north-western Cape where marginal or transitional forms usually occur. For separation of the different species of these ants the body setae and sculpture of the head and abdomen seem to be very important and for this purpose I have enlarged a small area of the vertex of the head and the middle of the first abdominal segment of each form to illustrate the sculpture and position of the setae. As the abdomen of ants is usually very variable due to shrinkage or swelling, depending on the method of preservation prior to pinning, the length of the insect as a whole is therefore approximate; the length from the apex of the clypeus to the apex of the petiole (or postpetiole) is more accurate, but it should be remembered that with old and fixed specimens this length would vary slightly according to the position in which the ant was fixed to the card.

In the first paragraph of each description the lengths of the various segments and their indices, most of them according to Brown (1949), Taylor (1968) and Sze-Li Hsu (1970), are given as follows (I have also included the cephalothoracic index, that is, the length of the head expressed as a percentage of the length of the truncus or $HL \times 100/WL$):

ED = Distance between compound eyes

CL = Clypeal length

FL = Frontal length

HFL = Hind femur length

HL = Head length (from the anterior margin of the clypeus to the posterior border; wherever a comparison is made in this paper, the mandibles are excluded unless otherwise stated)

L = Length from apex of clypeus to apex of petiole (or postpetiole)

LO = Length from hind margin of clypeus to middle ocellus.

MFL = Middle femur length

OD = Distance between hind ocelli

PL = Petiolar length (the length of the node only, excluding the peduncles)

PPL = Postpetiolar length (peduncles excluded)

SL = Scape length (from its apex to the tip of its basal lobe)

TL = Total length of insect including the mandibles

WL = Length of truncus (similar to that of Weber's, marked by arrows in the drawing)

CI = Cephalic index

CLI = Cephalothoracic index

FI = Frontal index

PI = Petiolar index

PPI = Postpetiolar index

SI = Scape index

TI = Thoracic index

DESCRIPTION

A. *Myrmicinae**Tetramorium solidum* Emery, 1886

(Figs 1-4, 27A, B)

♀ TL 3,68 mm; HL 1,04 mm; WL 1,00 mm; PL 0,28 mm; PPL 0,28 mm; HFL 0,92 mm; MFL 0,80 mm; ED 0,96 mm; SL 0,72 mm; CL 0,24 mm; FL 0,80 mm; L 2,84 mm; CI 107,7; CTI 104; CLI 341,6; FI 120; SI 64,3; TI 66; PI 128,6; PPI 164,3.

Arnold (1917) gives the colour as piceous, but the type specimen before me is rather dark burnt sienna to dark reddish brown; the antennae paler, the mandibles almost dark raw sienna. Fairly dull, the abdomen shining and very finely and superficially reticulate, the sculpture somewhat stronger on the base. Head longitudinally striate, the striae or rugae on the anterior part of the sides rather coarse, finely and superficially reticulate between the rugae. Clypeus with about 8 to 9 coarse longitudinal striae, continuous with those on the front and vertex. Mandibles striate and rather shining, the teeth black. Antennae microscopically and superficially reticulate—rugulose. Truncus very finely reticulate with some longitudinal striae or rugae superimposed dorsally, the sides obliquely striate; the nodes also finely reticulate and rugulose. Legs very superficially and finely reticulate and shining.

Pubescence short and decumbent more abundant on the legs and antennae. *Pilosity* sparse, consisting of a transverse row of curved setae on the anterior margin of the clypeus, a few long hairs on the frontal carinae, vertex and occipital corners of the head, the pro- and mesonotum, nodes and apical segments of the abdomen.

Head almost square, slightly wider than long, nearly two-fifths wider than the pronotum, the sides and hind margin almost straight. *Frontal area* indistinct, *eyes* small, with more than 60 facets, occupying about one-fifth of the length of the head, and situated in the middle of the sides.

Frontal carinae wide apart, extending to about the middle of the head. *Clypeus* almost flat above, the anterior face fairly high, its junction with the dorsum rounded, widely and deeply excised in the middle. Flagellum about three-tenths longer than the scape; the latter not reaching the hind margin by one-fifth of its length. The first joint of the flagellum as long as the second and third taken together; the 2nd to 5th slightly wider than long, the 6th about as long as wide, the rest longer than wide.

Truncus about four-ninths longer than wide over the pronotum and about three-fifths wider in front than behind over the bases of the spines, the thoracic sutures obsolete above, the meso-epinotal suture slightly indicated by a faint transverse ridge. In profile the dorsum forms a slight curve with the epinotum lower than the pronotum, the latter obtusely marginate in front. The *declivity*

of the epinotum almost vertical and transversely rugose, the dorsum nearly flat; the *spines* twice as long as wide at their bases and acute. *First node of petiole* a little more than one-fifth wider than long, seen from above the hind as well as the short front margin is almost straight, the node much narrower in front than behind, almost trapezoidal. In profile it is nearly quadrate, the front and hind faces vertical, the dorsum very slightly convex and about as high as wide behind; the subpetiolar process is present as a small acute tooth at the extreme base and pointing forward. *Second node* about as high as the first, seen from above two-fifths wider than long, the sides convex; in profile nearly one-fifth higher than long; the subpostpetiolar process developed as broad rounded lobes on each side. *Legs* moderately long. *Abdomen* truncate at base.

Type series: 2 ♂♂ (1 damaged). Locality and date unknown.

♀ (Figs 3, 4). TL \pm 5,6 mm; HL 1,18 mm; WL 1,70 mm; PL 0,34 mm; PPL 0,32 mm; HFL 1,12 mm; MFL 0,86 mm; ED 1,10 mm; OD 0,36 mm; LO 0,48 mm; SL 0,84 mm; CL 0,30 mm; FL 0,88 mm; L 3,76 mm; CI 110,2; CTI 69,4; CLI 346; FI 125; SI 64,6; TI 62,4; PI 147,1; PPI 212,5.

Burnt umber to castaneous red, mandibles, legs and antennae paler, light reddish brown, the swollen parts of the femora dark brown. Dull all over, the abdomen slightly shining. Head and dorsum of truncus longitudinally striate, finely reticulate between the striae, the scutellum of the mesonotum with somewhat finer striae. Epinotum finely reticulate-punctate and with some transverse rugae. Parapsidal furrows present, but not clearly visible from above (under low magnification). Sides of pro-, meso- and metathorax longitudinally striate, those on the latter oblique, the sides of the epinotum merely rugulose; the declivity reticulate-punctate and with some fine rugae superimposed. Both nodes finely reticulate-punctate, the first node with fine transverse rugae; the abdomen superficially and finely reticulate, the reticulation somewhat stronger on the basal portion. *Pubescence* and *pilosity* similar to those of the worker, the pubescent hairs longer on the whole body and also more abundant on the abdomen. Mesopleurae almost devoid of setae.

Head very slightly wider than long, almost square, the *eyes* occupy a little less than one-quarter of the length of the head. *Truncus* longer than the head, in profile the dorsum is almost straight, the spines long, about as long as wide at their bases, or slightly shorter than the length of the eyes. *First node of petiole* almost trapezoidal when seen from above, front margin straight with definite anterior corners, anterior and posterior faces vertical. In profile it is one-fifth higher than long, the dorsal face straight, the subpetiolar process present as a small acute tooth as in the worker. *Second node of petiole* about one-third higher than long; seen from above it is slightly more than twice as wide as long, the sides convex, not drawn out and flattened.

Material: 1 ♀ Santschi, 1916. Locality unknown. Specimen determined by G. Arnold.

Tetramorium solidum Emery subsp. *tuckeri* Arnold n. comb.

(Figs 5-7, 28A, B)

Tetramorium solidum Emery var. *tuckeri* Arnold, 1923 n. syn.

♂ (The head, truncus and first node of petiole intact, the second node and abdomen broken off.)

HL 1,40 mm; WL 1,44 mm; PL 0,38 mm; HFL 1,30 mm; MFL 1,10 mm; ED 1,16 mm; SL 0,94 mm; CL 0,34 mm; FL 1,06 mm; L (length from apex of clypeus to apex of petiolar node) 3,68 mm; CI 104,3; CTI 97,2; CLI 300; FI 109,4; SI 58,9; TI 59,7; PI 121,1.

Arnold gives the colour as black, but the type specimen in the collection is light castaneous to dark brick red, the antennae, mandibles and legs, except the middle portions of the femora which are of the same colour as the body, ferruginous. Almost dull, or with a very slight gloss, more shining than *solidum*, the sculpture similar to that of the latter, but stronger, the head more evenly striate, the declivity of the epinotum as coarsely and transversely striate (and reticulate).

The head is slightly wider than long, two-fifths wider than the truncus, the sides almost straight, the hind margin shallowly excised in the middle; the eyes large, occupying nearly two-sevenths of the length of the head. Frontal area indistinct, frontal sulcus obsolete, the frontal carinae wide apart, extending to about the middle of the head. Anterior face of clypeus less rounded than in *solidum*; the scapes not reaching the hind margin of the head by about one-quarter of their length.

Truncus about two-fifths longer than wide over the pronotum and about two-thirds wider in front than over the bases of the spines. The pronotum is margined in front, much more so than in *solidum* and the dorsum of the epinotum when seen in profile appears to be somewhat concave (slightly convex in the latter); the meso-epinotal suture is present as a wide notch and just behind this notch on the middle line is a small tooth-like prominence or tubercle. The pro-mesonotal suture which is absent in the type of the species and its other varieties, clearly demarcates the mesonotum. Sides of the epinotal dorsum almost parallel, the declivity vertical, the spines short, shorter than wide at the base and slightly longer than the episternal.

First node of petiole, seen from above, oval and slightly more than one-fifth wider than long, slightly wider behind than in front, both anterior and posterior margins convex, the latter somewhat angular in the middle; in profile it is quadrate as in *solidum*, the dorsum being almost straight, the hind face inclined backwards, forming an angle with the dorsum; subpetiolar process present as a minute rounded tooth or denticle.

Type: 1 ♂ Brehden, South West Africa, 20 December 1915 (R. W. E. Tucker).

In other specimens collected in Brehden, South West Africa (20 December 1915) (TL 5,0-5,2 mm; L 3,6 mm; PPI 200) the pro-mesonotal suture is almost

obsolete in the middle, but still indicated on each side of the pronotal disc. In this case the tooth-like tubercle behind the meso-epinotal suture is absent, so that the epinotal dorsum does not really appear concave; the spines (Figs 6B, C) are longer and resemble those of *solidum*; *first node of petiole* is more triangular, being slightly more than one-fifth wider than long (PI 122,2-123,5), the posterior margin is more rounded and not angular in the middle; in profile its anterior and posterior faces are almost vertical, the dorsal face slightly convex. *Second node of petiole* is nearly twice as wide and about three-eighths (excluding the subpostpetiolar process) higher than long, transversely rugose and finely reticulate between the rugae, the sides somewhat drawn out and flattened posteriorly; the subpostpetiolar process as broad rounded teeth.

The *abdomen* is superficially reticulate and shining, the reticulation stronger towards the base where it is also finely longitudinally rugulose (Fig. 28B).

Unfortunately Arnold did not state whether these specimens were collected from the same nests as the holotype; however, if more specimens become available from that area, I shall not be surprised if this subspecies is raised to specific rank.

In specimens from the north-western Cape (TL 5,16-5,8 mm; L 3,6-3,96 mm; PI 122,1-141,1; PPI 214,3-180) which are very similar to the specimens from South West Africa, the spines are almost of the same length (Fig. 6A), but the pro-mesonotal suture is very well indicated, making the mesonotum somewhat gibbous as in the type specimen. Although the abdomen in this case is also superficially reticulate, the reticulation is much closer and the striae on the base almost absent.

♀ (Figs 8, 9) TL 6,7 mm; HL 1,40 mm; WL 2,04 mm; PL 0,32 mm; PPL 0,32 mm; HFL 1,26 mm; MFL 1,0 mm; ED 1,20 mm; OD 0,34 mm; LO 0,54 mm; SL 0,90 mm; CL 0,36 mm; FL 1,04 mm; L 4,28 mm; CI 107,1; CTI 68,6; CLI 311,1; FI 115,4; SI 60; TI 58,8; PI 162,5; PPI 231,3.

Slightly larger than the female of *solidum*, with similar colour and sculpture, the striae forming a reticulation on the pronotum, the latter not so sharply margined laterally as in that species. Both nodes with transverse rugae which are much stronger than in *solidum*. Abdomen very finely and superficially reticulate or reticulate-coriaceous, the sculpture stronger on the basal third, where it is also finely longitudinally striolate. *Pubescence* and *pilosity* as in *solidum*.

Eyes somewhat bigger, occupying nearly two-sevenths of the length of the head; the hind ocelli closer together than in that species. *Truncus* with parapsidal furrows more clearly visible than in the latter, the suture between the scutellum and paraptera also clathrate; the suture between the meso-epimeron and mesosternite shallower but more clathrate.

The dorsum of the epinotum with oblique rugae, the declivity finely reticulate-punctate, dull and transversely striate. The *spines* short, about half as long as wide at their bases or about as long as the episternal. *First node of petiole* seen from above somewhat oval, the sides rounded, hind margin almost straight, front margin shallowly excised in the middle; it is about three-eighths

wider than long and also about as high as wide; in profile the dorsum is almost flat, the front and hind faces vertical; the subpetiolar process as in the worker. The *second node* is about twice as high and more than twice as wide as long, the sides less convex than in the workers from South West Africa and north-western Cape; and also drawn out and flattened posteriorly; the subpostpetiolar process more pointed than in *solidum*.

Type: 1 ♀ Brehden, South West Africa, 20 December 1915 (R. W. E. Tucker).

Tetramorium solidum Emery var. *signata* Emery, 1895

(Figs 37, 38)

♀ TL 4.40–4.8 mm; HL 1.16–1.25 mm; WL 1.16–1.28 mm; PL 0.32–0.36 mm; PPL 0.26–0.30 mm; HFL 1.04–1.18 mm; MFL 0.88–0.98 mm; ED 0.94–1.04 mm; SL 0.80–0.90 mm; CL 0.28–0.30 mm; FL 0.88–0.95 mm; L 3.0–3.40 mm; CI 100–101.7; CTI 97.7–100; CLI 320–335.7; FI 106.8–109.5; SI 67.9–71.4; TI 59.4–61.7; PI 111.1–112.5; PPI 160–164.3.

Brown to dark brown, the mandibles, antennae and legs paler, more yellowish brown, middle portions of the femora somewhat darker. Eyes, mandibular teeth and epinotal spines black. The inner margins of the frontal carinae, the front margin of the pronotum, front and hind margins of petiole and some of the rugae on the body also blackish. With a slight gloss, the abdomen fairly polished. Head longitudinally striate as in *tuckeri*, finely reticulate or reticulate-punctate between the striae. Median area of clypeus with about 8–9 striae, the middle one the strongest. Mandibles strongly longitudinally striate and shining. Pronotum reticulate-rugose, rest of truncus longitudinally rugose; finely reticulate-punctate between the rugae, the latter also longitudinally and somewhat obliquely arranged on the sides. First node reticulate-rugose, the reticulation not so clearly visible in some specimens, the second node merely rugose with some indistinct reticulation; both nodes finely reticulate-punctate between the rugae. Basal portion of the abdomen very finely reticulate, also finely and longitudinally rugulose and duller than the rest which is more superficially reticulate or reticulate-coriaceous. Legs and antennae microscopically reticulate, the scapes duller. *Pubescence* and *pilosity* as in *tuckeri*.

Head about as long as wide, about two-fifths wider than the pronotum, quadrate, the sides and hind margin almost straight. *Clypeus* with front margin slightly excised in the middle. Frontal carinae as in *tuckeri*, extending to about the middle of the head, the frontal area obsolete. *Eyes* occupy about one-quarter or slightly more of the length of the head, situated in the middle of the sides. The *scapes* falling short of the hind margin by about one-sixth of their length, they are about seven-tenths as long as the flagella; the 2nd to 6th joints nearly as long as wide, the rest longer than wide. *Truncus* about two-fifths longer than wide in front, the meso-epinotal suture clearly indicated on the dorsum as a transverse furrow, and on the sides as a clathrate impression. Pro-mesonotal

suture fairly clear dorso-laterally in one specimen, but obsolete in others. In profile the truncus and nodes are similar to those of *tuckeri*; the *spines* short, about as long as wide at the base, slightly longer than the episternal, the *epinotal declivity* almost vertical, transversely striate and finely reticulate-punctate between the striae. The *first node* triangular, with rounded apex, the sides and hind margin slightly convex; it is about one-eighth wider than long and about as high as wide. Seen from the side, the front and hind faces vertical, the dorsum slightly convex, the peduncle a little shorter than the node. The *second node* oval, about one-third wider and one-quarter higher than long; in profile the dorsal surface is rounded. Both the subpetiolar and subpostpetiolar processes as in *tuckeri*. *Legs* moderately long; *abdomen* truncate at base.

Material: 3 ♀♀ Willowmore, C.P., 1912 (H. Brauns). Specimens determined by G. Arnold.

Both these two forms are bigger than the type of the species, but may easily be recognized by the shorter spines and the first node which is rounded in front, whereas in *solidum* the node has a short, almost straight front margin; *tuckeri* on the other hand has a broad second node, almost twice as wide as long, while in *signata* the node is much narrower, being only one-third wider than long; in the latter form the pro-mesonotum is also reticulate or reticulate-rugose.

Tetramorium capense Mayr, 1865

(Figs 35, 36)

♀ TL 3,60 mm; HL 0,92 mm; WL 0,94 mm; PL 0,20 mm; PPL 0,20 mm; HFL 0,74 mm; MFL 0,64 mm; ED 0,76 mm; SL 0,66 mm; CL 0,20 mm; FL 0,72 mm; L 2,48 mm; CI 91,3; CTI 97,9; CLI 330; FI 105,6; SI 78,6; TI 57,4; PI 120; PPI 140.

Yellowish red, the mandibular teeth and eyes black, abdomen slightly more brownish; body with a faint gloss, the legs and antennae more shining, the abdomen very shining. Head longitudinally striate in the middle, rugoso-striate and also reticulate on the sides, finely reticulate between the striae and rugae. Clypeus with about 6 to 8 longitudinal striae, the median one the strongest. Mandibles longitudinally striate and moderately shining. Truncus and nodes finely reticulate, almost reticulate-punctate, with longitudinal rugae superimposed, some of the rugae connected by anastomoses, almost forming an indistinct reticulation. Sides of truncus also with longitudinal rugae, the lower rugae rather coarse, the fine reticulation on the meso- and epipleurae somewhat bigger than on the dorsum. Abdomen very superficially and finely reticulate, almost reticulate-coriaceous. Antennae and legs microscopically reticulate-rugulose, the sculpture somewhat stronger on the scapes. *Pubescence* almost as in *solidum*, the abdomen appears to be almost glabrous. *Pilosity* long erect, yellowish, more abundant on the head and abdomen than in the latter species; there are at least six setae on the petiole and four on the postpetiole.

Head one-eleventh longer than wide and about one-third wider than the

pronotum, the sides slightly convex, the hind margin straight; as wide in front as behind. *Frontal area* fairly well indicated as a triangular impression, the *frontal carinae* somewhat convergent in front, parallel behind and extending to about the posterior two-ninths of the head, hardly forming a demi-scribe. *Clypeus* fairly flat in the middle, the front margin slightly convex, with a very small wide emargination in the middle. *Eyes* small, with about thirty facets, occupying about one-eighth of the length of the head and situated in the middle of the sides. *Scapes* shorter than the head, not reaching the hind margin by about one-eighth of their length, the flagellum as long as the head, the 2nd-4th joints slightly wider than long, the 5th-8th about as long as wide and the rest longer than wide, the last joint the longest.

Truncus similar to that of *peringueyi*, about five-twelfths longer than wide and about seven-elevenths wider in front than over the bases of the spines, somewhat constricted between the meso- and epinotum, the sutures obsolete above. In profile the dorsum is moderately convex with the epinotum lower than the mesonotum as in the other species already described; the *spines* long and acute, about three-eighths longer than wide at the base and about as long as the interval between their bases. (In *solidum* the spines are narrower at their bases.) Otherwise as in *peringueyi*. *First node of petiole* one-third higher and about one-sixth wider than long, seen from above it appears cuneiform, almost trapezoidal, widest over the posterior third, the anterior margin straight. Seen in profile truncate in front, the anterior face nearly as long as the oblique hind face, the dorsal face almost straight and much shorter than in *solidum* and shorter than the peduncle (in the latter species it is longer than the peduncle); the subpetiolar process as a minute rounded tooth. The *second node* as long as the first, about one-fourth wider than long and about as high as wide, almost oval when seen from above; in profile the dorsum is much more convex than in *solidum*, the subpostpetiolar process without a lobe on each side. *Abdomen* not truncate at base but rounded. *Legs* moderately long.

Type: Locality and date unknown.

Very similar to *peringueyi* Arnold *dichroum* Santschi, but differs from it by the smaller eyes, the finer sculpture of the truncus and nodes, the lighter colour and by the pilosity which is less abundant, especially on the abdomen. It differs from all the species described in this paper by the truncate first node and by the abdomen which is rounded at the base. According to Arnold (1917, 1923) it may be separated from *popovici* by the dorsal face of the first node which is as wide as or wider than long. I have not seen *popovici* in life and cannot therefore comment on this point; it seems however if the latter could be a synonym of *capense*.

Tetramorium peringueyi Arnold, 1923

(Figs 19, 20, 31A, B)

♂ TL 4.60-4.80 mm; HL 1.20 mm; WL 1.24-1.26 mm; PL 0.34 mm;
PPL 0.34-0.36 mm; HFL 1.12 mm; MFL 1.0 mm; ED 1.10 mm; SL 0.90 mm;

CL 0,26 mm; FL 0,94 mm; L, 3,40–3,32 mm; CI 106,7; CTI 96,8–95,2; CLI 384,6; FI 117; SI 70,3; TI 62,9–63,5; PI 129,4–135,3; PPI 158,8–155,6.

Pale to dark brick red, the middle portion of the head somewhat darker, the abdomen brown to mahogany with the basal portion paler. Mandibular teeth black. Head, truncus, petiole and basal third of the abdomen slightly shining, rest of abdomen and legs shining. Head coarsely and longitudinally striate, widely reticulate on the sides and at the back, the striae on the occiput divergent on each side. Mandibles coarsely longitudinally striate and shining. Middle portion of the clypeus with about 6 to 8 striae, the median one not particularly stronger than the others. Truncus rugoso-reticulate dorsally, the sides rugoso-striate; the epinotal declivity strongly and transversely striate and shining. Sides and dorsal surfaces of both nodes rugoso-reticulate, the floors of the reticulation and the spaces between the striae like those of the head and truncus very finely and superficially reticulate; the rugae on the posterior faces of both nodes somewhat transversely arranged. Abdomen very superficially reticulate and shining, the sculpture on the basal third stronger, the striolation longitudinally arranged. Tibiae and scapes finely and longitudinally striolate and fairly dull, rest of legs superficially sculptured and shining. *Pubescence* present only on the flagellum. *Pilosity* long, fairly abundant all over including the legs, erect and yellowish white in colour; some of the hairs on the head, especially those on the anterior border of the clypeus longer than the rest.

Head about one-sixteenth wider than long and about three-eighths wider than the pronotum, the sides parallel, the hind margin straight. *Frontal area* indistinct, the *frontal carinae* wide apart and divergent behind, extending to about the middle of the head, the clypeus widely and fairly deeply emarginate in front. The *eyes* occupy one-fifth of the length of the head, situated in middle of the sides. *Scapes* fall short of the hind margin by about one-sixth of their length; all the joints of the flagellum longer than wide, except the third which is slightly wider than long. *Truncus* about three-eighths longer than wide over the pronotum and more than twice as wide here than over the bases of the spines. *Thoracic sutures* obsolete above; on the sides the pro-mesonotal suture is fairly well indicated, the meso-epinotal suture is represented by a wide impression, the alitrunk being slightly constricted in this area. Pronotum submarginate in front, the neck also rugoso-reticulate, the rugae transversely arranged. In profile the dorsum of the alitrunk forms a wide curve, with the epinotum lower than the pro-mesonotum. The *spines* long, slightly more than twice as long as wide at the base and slightly longer than the interval between their bases, thin and acute, directed outwards and slightly upwards.

First node of the petiole trapezoidal, seen from above much wider behind than in front, about one-quarter wider than long, front and hind margins straight; in profile it is about as high as wide, the front and hind faces vertical, the dorsal face flat, the peduncle about as long as the node, the subpetiolar process very similar to that of *solidum*. The *second node* is oval, the sides rounded, about one-third wider and seen from the side about one-sixth higher than long, rounded,

the subpostpetiolar process as in *solidum*. *Abdomen* truncate at the base. *Legs* moderately long.

Type series: 2 ♂♂, Kimberley, 1916 (G. Arnold).

***Tetramorium peringueyi* Arnold ssp. *dichroum* Santschi n. comb.**

(Figs 21, 11, 32A, B)

Tetramorium solidum Emery var. *dichroum* Santschi, 1932 n. syn.

♂ TL 3,76–3,80 mm; HL 1,02–1,04 mm; WL 1,0–1,04 mm; PL 0,30 mm; PPL 0,24 mm; HFL 0,84 mm; MFL 0,76 mm; ED 0,90–0,92 mm; SL 0,68–0,70 mm; CL 0,22–0,24 mm; FL 0,80 mm; L 2,72–2,76 mm; CI 105,9; CTI 102–100; CLI 372,7–350; FI 112,5–115; SI 62,9–63,6; TI 66–63,5; PI 120; PPI 175.

Light burnt sienna (Santschi described it as red), the head, abdomen, femora and tibiae darker, dark burnt sienna; mandibular teeth black. Head longitudinally striate the striae finer than in *peringueyi*; on the sides and at the back with some wide reticulations; very finely reticulate-punctate between the striae. Middle area of clypeus with 6 to 8 striae, the median one stronger than the rest. Dorsum of the truncus longitudinally rugose, with some transverse anastomoses, especially on the epinotum and frontal portion immediately behind the neck; sides longitudinally rugose. Both nodes reticulate-rugose, almost as in *peringueyi*, the spaces between the striae, as in the case of the head and truncus, finely reticulate-punctate. Abdomen finely and superficially reticulate, the reticulation slightly more pronounced than in the latter species, fairly coarse on the basal third, where it is also longitudinally striolate. Body only slightly shining, somewhat duller than *peringueyi*; abdomen except its basal part more shining than the head and truncus. Antennae and legs microscopically reticulate-punctate and slightly shining. *Pilosity* and *pubescence* similar to that of the latter.

Head very slightly (about one-twenty-secondth) wider than longer and about two-fifths wider than the alitrunk, the sides parallel, the hind margin slightly concave in the middle. *Frontal area* indistinct, the *frontal carinae* wide apart, extending to about the middle of the head; *clypeus* widely and deeply emarginate in the middle; *scapes* slightly shorter than in *peringueyi*, falling short of the hind margin by about one-fifth of their length; the flagellum nearly two-ninths longer than the scape, the 3rd joint a little wider than long, the 2nd to 5th as wide as long, the rest longer than wide. *Eyes* situated in the middle of the sides, occupying about one-fifth of the length of the head. *Truncus* two-fifths longer than wide and nearly two-thirds wider in front than over the bases of the spines. The sutures obsolete above, only indicated on the sides, the meso-epinotal by a wide impression so that the truncus appears somewhat constricted in this area when seen from above. In profile the dorsum forms a wide curve with the *epinotum* lower than the pro-mesonotum, the vertical declivity transversely

striate; the *spines* nearly twice as long as wide at the base (or about as long as the interval between their bases).

First node trapezoidal, seen from above the margins straight (the sides slightly convex in *peringueyi*), only a little more than one-eighth wider behind than long and about as high as wide, the peduncle shorter than the node (nearly as long in *peringueyi*), seen from the side the front and hind faces vertical, the dorsal face very slightly convex; the subpetiolar process as in the latter species. The *second node* about three-sevenths wider than long, oval, the sides rounded, seen from the side about two-sevenths higher than long, the subpost-petiolar process as in *peringueyi*. *Abdomen* and *legs* as in the latter.

Type series: 3 ♀♀, Kimberley, 1924 (G. Arnold).

It is quite obvious that according to sculpture, setae and occurrence, this form is a subspecies of *peringueyi* and not a variety of *solidum*; in life it is very similar to the first although much smaller.

***Tetramorium aspinatum* n.sp.**

(Figs 10-13, 29A, B)

♀ TL 3.88-4.0 mm; HL 1.02-1.04 mm; WL 1.0-1.04 mm; PL 0.26-0.28 mm; PPL 0.24 mm; HFL 0.90-0.96 mm; MFL 0.74-0.78 mm; ED 0.86-0.90 mm; SL 0.76-0.78 mm; CL 0.24-0.26 mm; FL 0.76-0.78 mm; L2,92-2.94 mm; CI 100-103.9; CTI 98.1-104; CLI 323-333.3; FI 113.2-118.4; SI-71.7-74.5; TI 58.8-64; PI 121.4-123.1; PPI 116.7-183.3.

Dark brown or blackish brown, legs and peduncle of the first node paler in colour, antennae and mandibles reddish, mandibular teeth and eyes black. Head, truncus and nodes moderately shining, abdomen very shining. Head longitudinally striate as in *solidum*, the striae on the cheeks stronger than on the rest of the head, finely reticulate between the striae. Median area of clypeus with 6 to 9 striae, the middle one somewhat stronger than the rest. Mandibles striate and shining. Truncus finely reticulate or reticulate-punctate with fine longitudinal rugae superimposed, those on the lower parts of the meso- and epipleurae stronger. Both nodes and basal third of the abdomen also finely reticulate or alutaceous, the reticulation stronger on the sides of the nodes and on the peduncle, almost superficial on the abdominal base, very superficial on the rest of the abdomen; the nodes of some specimens however almost reticulate-rugulose. Legs and antennae microscopically reticulate and shining.

Pubescence consists of fairly long sparse, yellowish-white decumbent hairs, transversely arranged on the head and truncus, more abundant on the flagellum. *Pilose hairs* present as follows: a transverse row on the anterior margin of the clypeus, one hair in front on each frontal carina, two on the vertex, one on each occipital corner, some on the 2nd to last abdominal segments and on the ventral part of the body. (In *solidum* long setae occur also on the truncus and nodes.)

Head about as long as wide, or very slightly wider than long and about one-third to five-twelfths wider than the truncus, the sides parallel, the hind

margin straight, occipital angles rounded. *Frontal area* indistinct; *frontal carinae* wide apart, divergent behind, extending to the middle of the head. *Clypeus* with front margin only slightly excised in the middle, therefore appearing to be longer than that of *solidum*. *Eyes* situated in the middle of the sides occupying about one-quarter of the length of the head. *Scapes* falling short of the hind margin by about one-eighth of their length, the flagellum nearly one-quarter longer than the scape; 2nd to 3rd joints about as long as wide, the rest longer than wide, the first joint almost as long as the ninth. *Truncus* about two-fifths longer than wide, narrower behind than in front, narrowed in the region of the meso-epinotal suture, epinotal dorsum rounded from side to side, all the sutures dorsally absent except for a slight transverse depression between the meso- and epinotum. In profile the dorsum forms a wide curve, with the *epinotum* lower than the pro-mesonotum; the declivity reticulate, oblique and forming a rounded angle with the dorsum; *spines* absent or represented by a small tubercle on each side. The *first node* seen from above almost triangular, with the angles rounded, the front margin and sides almost forming a semicircle in some specimens, about one-fifth wider than long and about as high as wide; seen from the side the front and hind faces vertical; the peduncle almost as long as the node, the subpetiolar process present as a minute tooth in front. The *second node* oval, from three-eighths to almost twice as wide as long; seen from the side about one-seventh higher than long, the subpostpetiolar process somewhat more pointed than in *solidum*. *Legs* as in that species. *Abdomen* truncate at base.

Type series: 4 ♀♀, South African Museum. Port Nolloth, 20 April 1963 (J. J. Cillie).

3 ♀♀, Plant Protection Research Institute, Pretoria. Same locality and date.

♀ (Figs 12, 13) TL 6,6 mm; HL 1,32 mm; WL 2,0 mm; PL 0,38 mm; PPL 0,40 mm; HFL 1,32 mm; MFL 1,08 mm; ED 1,22 mm; OD 0,38 mm; LO 0,54 mm; SL 0,96 mm; CL 0,36 mm; FL 0,96 mm; L 4,40 mm; CI 110,8; CTI 65,0; CLI 294,4; FI 129,8; SI 66,7; TI 62,0; PI 142,1; PPI 195.

Blackish brown, abdomen and neck brown, antennae, mandibles, legs, except the middle portions of the femora which are blackish brown, reddish; mandibular teeth black. Whole body moderately shining. Head and truncus, except the epinotum longitudinally striate, the striae somewhat coarser on the sides; epinotum transversely striate, finely reticulate between the striae, the reticulation on the head as dense as on the truncus. Clypeus with the median stria somewhat stronger than the rest. Sutures between meso-epimeron and mesosternite, as well as that between the scutellum and paraptera clathrate; parapsidal furrows clearly visible from above. Both nodes finely reticulate-rugulose, with some fine transverse rugae superimposed, on the second node the rugae present mostly on its posterior half. Abdomen very finely reticulate-alutaceous, the reticulation stronger on the basal third, elsewhere superficial or even shagreened. Legs microscopically reticulate, the fore tibiae appearing duller. *Pubescence* fairly long, decumbent, similar to *solidum*, but slightly more

abundant on the abdomen. *Pilose hairs* as in that species. Meso-epimeron and mesosternite almost glabrous, only with some hairs round the edges.

Head about one-tenth wider than long and about one-seventh wider than the truncus, almost square, the sides and hind margin straight. *Frontal area* indistinct, anterior margin of *clypeus* only slightly excised in the middle. *Eyes* occupying about one-quarter of the length of the head; situated in the middle of the sides; *scapes* falling short of the hind margin by a fraction of their length; all the joints of the flagellum longer than wide, except the 3rd which is about as long as wide. *Truncus* about three-eighths longer than wide; in profile the scutellum is somewhat gibbous, its dorsum slightly higher than that of the mesonotum (the same height in *solidum*). *Epinotal teeth* almost obsolete, represented by two very small broad dents, shorter than the episternal teeth. *Epinotal declivity* vertical, finely reticulate and strongly and transversely striate. *First node of the petiole* rounded, almost three-ninths wider than long and about as high as wide; in profile, both faces somewhat oblique, the peduncle about as long as the node. The *second node* oval, about twice as wide as long and one-sixth wider than high, the subpetiolar and subpostpetiolar processes as in the worker. Otherwise like the female of *solidum*.

Type: 1 ♀, South African Museum. Port Nolloth, 20 April 1963 (J. J. Cillie).

This species is very similar to *solidum* in size and body shape but may easily be recognised by the absence of any spines. In life it responds in the same way as the latter and seems to be present only in sandy soil along the coastal areas in the west and probably also further inland.

Tetramorium rutilum n.sp.

(Figs. 14-18, 30A, B)

♂ TL 4.4-4.8 mm; HL 1.14-1.22 mm; WL 1.18-1.24 mm; PL 0.26-0.28 mm; PPL 0.26-0.28 mm; HFL 1.04-1.12 mm; MFL 0.88-0.90 mm; ED 1.00-1.04 mm; SL 0.80 mm; CL 0.26-0.28 mm; FL 0.86-0.94 mm; L 3.08-3.28 mm; CI 103.3-103.5; CTI 90.3-96.6; CLI 328.6-346.1; FI 113.6-115.3; SI 63.5-67.8; TI 61-62.7; PI 142.9-146.2; PPI 176.9-178.6.

Brick red, the clypeus, anterior margin of the cheeks, coxae especially the front coxae, mesosternum, epinotal sides, scapes, femora, tibiae and posterior third or so of abdomen piceous; eyes, inner margins of frontal carinae, mandibular teeth and spines pitch black. Moderately shining, abdomen slightly more polished than the rest of the body. (In some specimens from the same locality, the insects are very shining, the dorsal surfaces of the nodes are just as superficially sculptured as the abdomen, and the striae on the head very inconspicuous.) Head finely reticulate and also finely and longitudinally striate, the striae on the cheeks and clypeus stronger than on the rest of the head (which appears merely finely reticulate-striate.) Mandibles striate and shining.

Truncus and nodes of the petiole very finely and somewhat superficially reticulate, almost reticulate-rugulose, the reticulation stronger on the sides;

the meso- and epipleurae also finely and obliquely rugoso-striate as in *aspinatum*. Abdomen alutaceous. Legs and antennae microscopically rugulose, the legs moderately shining, the sculpture coarser on the scapes which are dull. *Pubescence* short, scanty, decumbent and inconspicuous, more abundant on the antennae. *Erect pilosity* exactly as in *aspinatum*.

Head very slightly wider than long and about two-fifths wider than the thorax, quadrate, the sides and hind margin straight. *Frontal area* indistinct, *frontal carinae* wide apart, divergent behind, extending nearly to the middle of the head. Front margin of the *clypeus* with a narrow angular emargination in the middle; *eyes* placed in the middle of the sides and occupying about one-quarter of the length of the head. Flagellum one-fifth longer than the *scape*, the latter falling short of the hind margin of the head by about one-sixth of its length; 2nd to 8th joints of the flagellum as long as wide, the rest longer than wide. *Truncus* about three-eighths longer than wide, much wider in front than behind, all the sutures obsolete above, the meso-epinotal suture sometimes indicated by a faint transverse impression. In profile the truncus is similar to that of *aspinatum*, the demarcations between the mesonotum and mesosternum and between the meso- and episternum clathrate. The *declivity* of the epinotum sculptured as the thorax, with some fine transverse rugae superimposed. *Spines* present as short, broad triangular teeth, about as long as the episternal and about half as long as the interval between their bases. *First node*, seen from above, semicircular, the hind margin almost straight or slightly convex, the posterior angles rounded, about one-third wider than long; seen from the side almost as high as wide, anterior face oblique, posterior face vertical, the peduncle only very slightly longer than the node, the subpetiolar process absent or present as a very minute tubercle. *Second node* about four-ninths wider than long, oval, seen from the side, about three-tenths higher than long, the subpostpetiolar process present as a broad rounded tooth on each side, more pointed than in *aspinatum*. *Abdomen* truncate at base. *Legs* as in that species.

Type series: 3 ♂♂, South African Museum. Vanrhynsdorp, C.P., 19 April 1963 (J. J. Cillie).

4 ♀♀, Plant Protection Research Institute, Pretoria. Same locality and date.

In some of the smaller workers the head is nearly one-twelfth wider than long and somewhat longer than the truncus, the following measurements being representative: TL 4,32 mm; HL 1,06 mm; WL 1,00 mm; PL 0,26 mm; PPL 0,24 mm; HFL 0,98 mm; MFL 0,84 mm; ED 0,94 mm; SL 0,72 mm; CL 0,26 mm; FL 0,76 mm; L 2,88 mm; CI 107,5; CTI 106; CLI 338,5; FI 123,7; SI 63,2; TI 72,0; PI 130,8; PPI 175.

In some specimens collected near Bitterfontein, Cape Province (9 October 1959, A. J. Prins) the postpetiolar process forms a minute acute tooth at the extreme base of the petiolar peduncle; the colour being similar to that described above, but in the same species from Klawer, Cape Province (19 April 1963, J. J. Cillie) the colour is much paler, yellowish red, the basal part of the abdomen yellowish to ochreous; the truncus is about as long as the head or slightly

shorter (CTI 100–103,8), the spines of similar length but the head and truncus smaller in comparison to the Vanrhynsdorp specimens (HL 1,08–1,10 mm; WL 1,04–1,08 mm; CI 101,1–101,8; TI 61,8–63,5); both nodes of similar length but somewhat narrower (PL 0,26 mm; PPL 0,26 mm; PI 130,8–138,5; PPI 169,2); the postpetiolar process resembles that of the Bitterfontein forms. In one nest found near Vanrhynsdorp (24 August 1962, J. J. Cillie) the workers are much smaller (TL 3,68–3,80 mm; L 2,64–2,72 mm; HL 1,0–1,02 mm; WL 1,0–1,02 mm; PL 0,24–0,26 mm; PPL 0,20 mm; HFL 0,88–0,90 mm; MFL 0,76 mm; ED 0,86–0,88 mm; SL 0,70–0,72 mm; CL 0,24–0,26 mm; FL 0,76 mm; CI 103,9–104; CTI 100; CLI 315,4–333,3; FI 113,2–115,8; SI 67,3–67,9; TI 62–62,7; PI 130,8–133,3; PPI 200–210). The colour is paler, of a yellowish brown instead of red, the spines (Fig. 15) a little longer, the head as long as the truncus and the second node more than twice as wide as long, otherwise like the type of the species.

♀ (Figs 17,18) TL 6,0 mm; HL 1,22 mm; WL 1,76 mm; PL 0,28 mm; PPL 0,30 mm; HFL 1,16 mm; MFL 0,98 mm; ED 1,14 mm; OD 0,36 mm; LO 0,52 mm; SL 0,86 mm; CL 0,34 mm; FL 0,88 mm; L 3,84 mm; CI 109,8; CTI 69,3; CLI 305,9; FI 128,4; SI 64,2; TI 64,8; PI 171,4; PPI 233,3.

Brownish red, vertex of the head paler, posterior half of abdomen, clypeus, anterior margins of cheeks, middle portions of scapes, femora and tibiae as well as the meso- and episterna and ventral part of abdomen brownish black. Mandibular teeth, eyes, inner margins of the frontal carinae, a small area just in front of the pro-mesonotal suture, the metanotum, margins of the scutellum and paraptera, margins of the mesonotum above the wing roots and the tips of the spines pitch black. Head and truncus, except the scutellum and epinotum finely longitudinally striate, the striae on the cheeks and clypeus stronger; the scutellum transversely rugose, very finely reticulate between the striae, the epinotum and both nodes finely reticulate or reticulate-rugulose with some fine transverse rugae superimposed, especially on the posterior part of the first node. The sides of the truncus also finely reticulate and longitudinally rugoso-striate, the rugae indistinct in the region near the spines, the suture between the paraptera and scutellum as well as that between the meso-epimeron and mesosternum clathrate. Abdomen finely and superficially reticulate over the basal area, elsewhere aciculate. Body fairly shining, abdomen somewhat more polished, the sculpture of this insect weaker than in *aspinatum*. Antennae and legs microscopically reticulate-rugulose and shining, the scapes duller.

Pubescence yellowish, shorter and more inconspicuous than in the latter, sparser on the abdomen. *Pilosity* of head and abdomen the same as in that species, the truncus seems to be without any pilosity.

Head slightly more than one-tenth wider than long and one-seventh wider than the truncus. *Scapes* falling short of the hind margin by one-eleventh of their length; *eyes* occupying three-elevenths of the length of the head. *Epinotal declivity* nearly vertical, finely reticulate and also coarsely and transversely striate; the *spines* longer than in *aspinatum*, forming definite triangular teeth, as

long as the episternal. *First node* two-fifths wider than long and as high as wide, seen from above the sides and front margin almost forming a semi-circle, hind margin slightly convex; in profile it is much thinner than in *aspinatum*, the hind face vertical, the front face slightly oblique, the peduncle one-quarter longer than the node, the postpetiolar process obsolete. *Second node* slightly more than twice as wide and nearly two-fifths higher than long, otherwise like the female of *aspinatum*, except that it is somewhat smaller.

Type: 1 ♀, South African Museum. Same date and locality as ♂.

Quite distinct from the other forms in this group by its red colour and finely sculptured, almost smooth integument. The distribution seems to be the same as for *aspinatum*.

Tetramorium jauresi Forel, 1914

(Figs 39, 40)

♀ TL 4,28 mm; HL 0,96 mm; WL 1,24 mm; PL 0,28 mm; PPL 0,24 mm; HFL 0,74 mm; MFL 0,64 mm; ED 0,74 mm; SL 0,62 mm; CL 0,24 mm; FL 0,72 mm; L 2,88 mm; CI 93,8; CTI 77,4; CLI 283,3; FI 102,8; SI 68,9; TI 48,4; PI 100; PPI 141,7.

Light brown to brown, mandibles, flagellum, tarsi and basal half of second abdominal segment paler, more yellowish. Whole body with a slight gloss, the nodes somewhat duller, apical part of abdomen more shining. Head longitudinally striate in the middle, the median one the strongest, and continuing over the clypeus where it is much weaker developed, the cheeks reticulate-rugose, the sides above the eyes rugulose, the rugae just above the eyes stronger, finely reticulate or reticulate-punctate between the rugae and striae. Mandibles longitudinally and superficially striate, also superficially reticulate-punctate between the striae and shining. Truncus reticulate-rugulose with indistinct longitudinal rugae superimposed; anterior portion of pronotum, dorso-lateral areas of epinotum and probably also of the pro-mesonotum indistinctly rugoso-reticulate; some stronger longitudinal striae appear on the lower part of the epipleurae; a small oval area on the middle of the mesonotum dorsum very shining with the sculpture effaced, the reticulation very superficial. Epinotal declivity finely reticulate, also transversely striate and shining. Both nodes finely reticulate-punctate and indistinctly rugose, the first node also somewhat reticulate-rugose on the dorso-lateral and anterior sides, a small area over its middle has the sculpture effaced and appears very shining. Abdomen very finely reticulate-rugulose, especially the basal half; where it is dull. Rest of abdomen shining. *Pubescence* very scanty, more abundant on the legs and antennae, almost absent from the rest. *Pilosity* consisting of some long erect yellowish hairs on the clypeus, vertex and occiput of the head and the abdomen, similar to *capense*, but only two on the truncus and second node, the first node seems to be devoid of pilose hairs.

Head longer than wide (about one-fifteenth when measured over the eyes.

Arnold (1917) mentions one-fifth; this could be true if the mandibles are included) and one-third wider than the pronotum, quadrate, the sides almost parallel, the hind margin slightly concave. When viewed from above the mandibles extend further beyond the anterior margin of the clypeus than in *solidum* and its varieties, making the head appear even longer. *Frontal area* present as an indistinct triangular impression, traversed by the median stria. *Frontal carinae* almost parallel, extending nearly to the hind margin, but not forming scrobes. *Eyes* fairly convex, situated in the middle of the sides and occupying nearly one-fifth of the length of the head. *Scapes* not reaching the hind margin of the head; they are about three-fifths the length of the flagellum; 2nd-8th joints wider than long, the rest longer than wide.

Truncus about twice as long as wide and about two-thirds wider over the pronotum than over the bases of the spines, the shoulders less pronounced than in *solidum*, the pro-mesonotal suture faintly indicated as a very shallow impression; meso-epinotal suture indicated on the sides where the truncus is also somewhat constricted, the demarcation of the two segments on the dorsum indicated by short longitudinal rugae; the mesonotum appearing margined on each side. In profile the dorsum is less convex, almost flat, the *spines* short, as long as the episternal, directed upwards, slightly shorter than wide at the base and much shorter than the interval between their bases; the *declivity* of the epinotum almost vertical and shorter than the dorsum. The *first node* seen from above almost conical, the sides, hind and front margins convex, as long as wide, narrowed upwards towards the median line; when seen from the side, the front and hind faces almost vertical, about one-fifth higher than long, the peduncle shorter than the node, the subpetiolar process present as a rounded tooth pointing forward. *Second node* oval when viewed from above, about three-tenths wider than long and about as high as wide; from the side the dorsum is convex and the subpostpetiolar process almost as in *peringueyi*. *Abdomen* only narrowly truncate at the base. *Legs* fairly short, the femora more swollen than in *solidum*.

Material: 1 ♀, Park Ryne, Natal, 1914 (G. Arnold).

The locality is the same as that of the type.

Very different from the other species mentioned here by the longer head and the first node which is narrowed upwards. It has been collected only along the south coast of Natal.

KEY FOR THE IDENTIFICATION OF THE SPECIES

In view of the fact that some of the early myrmecologists have been in error concerning the length of the epinotal spines of these species, it is quite clear that the keys for identification of these groups of ants (Arnold 1923: 244-245, couplets 83-102) should be altered as follows:

- | | | |
|------|----|---|
| (96) | 83 | Epinotal spines or teeth distinctly longer than wide at the base (or about as long in <i>vexator</i> and <i>solidum signata</i>) |
| (91) | 84 | No demiscrobes present (or only a very slight trace of it, hardly described as demiscrobes) |

- (88) 85 Pronotum finely striate or rugoso-striate, not really reticulate, especially on the dorsum; hairs sparse
- (87) 86 Dorsal face of the first node distinctly longer than wide. Dark yellowish red *popovici* Forel
- (86) 87 Dorsal face of the first node as wide as or wider than long
- (87b) 87a Eyes small with about 30 facets; head longer than wide, first segment of abdomen with pilose hairs, rounded at the base, not truncate. First node truncate in front. Pale ochreous. *capense* Mayr and the var. *braunsi* Forel
- (87a) 87b Eyes larger, with about 60 or more facets. Head wider than long. First abdominal segment devoid of any pilose hairs, truncate at the base. First node not truncate in front. Dark reddish brown. *solidum* Emery
- (85) 88 Pronotum reticulate or rugoso-reticulate. Hairs abundant
- (90) 89 Nodes of petiole dull
- (89b) 89a Whole dorsum of pro-mesonotum reticulate, larger species 4.60-4.68 mm. Spines long, more than twice as long as wide at their bases (longer than the interval between their bases) *peringueyi* Arnold
- (89a) 89b Dorsum of pro-mesonotum longitudinally rugose or with some indistinct transverse anastomoses; small species 3.7-3.8 mm; spines shorter, less than twice as long as wide (shorter than the interval between their bases) *peringueyi* Arnold *dichroum* Santschi
- (89) 90 Nodes of petiole shining *grassi* Emery
- (84) 91 Demiscrobe present
- (93) 92 1st node cuneiform *vexator* Arnold
- (92) 93 1st node not cuneiform, with a distinct dorsal as well as anterior and posterior faces
- (95) 94 Base of abdomen not sculptured. Head (excluding the mandibles) nearly one-sixth longer than wide. Clypeus with a median carina. *guineense* Fabricius
- (94) 95 Basal two-fifths of abdomen dull and longitudinally striate. Head (excluding mandibles) hardly longer than wide. Clypeus without a carina. *bacchus* Forel
- (83) 96 Epinotal spines or teeth not longer than wide at the base. (In *vexator* they are about as wide, or slightly longer, but in this species the first node is cuneiform, a definite demiscrobe is present and the pilosity is very sparse)
- (108) 97 Larger species not less than 3.5 mm long
- (103) 98 No trace of scrobes
- (101) 99 Epinotal teeth longer than the episternal
- (100b) 100a Second node about twice as wide as long; pro-mesonotal suture usually fairly distinct (in some specimens not so clearly indicated). Pro-mesonotum more or less without a distinct reticulation, merely rugose, also finely reticulate-punctate between the rugae. *solidum* Emery *tuckeri* Arnold
- (100a) 100b Second node only about one-third wider than long; pro-mesonotal suture usually obsolete (in some specimens indicated to a certain extent dorso-laterally). Pro-mesonotum with a more definite reticulation (also finely reticulate-punctate between the rugae) *solidum* Emery *signata* Emery
- (99) 101 Epinotal teeth not longer than the episternal or almost entirely absent (in *solidum* Emery *tuckeri* Arnold the spines are sometimes just as long as the episternal, but in this case the pro-mesonotal suture is clearly visible)
- (101b) 101a Epinotal teeth obsolete, or represented by a very small tubercle or a small ridge on each side. *aspinatum* n.sp.
- (101a) 101b Epinotal teeth present

- (102b) 102a Head as wide as or slightly wider than long; first node not narrowed upwards towards the median line, broad above and wider than long. Colour reddish *rutilum* n.sp.
- (102a) 102b Head longer than wide; first node narrowed upwards towards the median line, about as wide as long, colour brownish *jauresi* Forel
- (98) 103 A more or less distinct demiscrobe present. (The species in this category may be distinguished from *vexator* by either abundant pilosity on the abdomen or by the first node which has a definite dorsal surface)

B. Formicinae

Camponotus subgenus *Mayria* Forel

Camponotus namacolus n.sp.

(Figs 23, 24, 33A, B)

♀ TL 5,0–5,17 mm; HL 1,06–1,08 mm; WL 1,64–1,66 mm; PL 0,32 mm; HFL 0,74–0,80 mm; MFL 1,04 mm; ED 0,68–0,70 mm; SL 1,04–1,06 mm; CL 0,30–0,32 mm; FL 0,76 mm; L 3,20–3,24 mm; CI 87,2–90,7; CTI 64,6–65,1; CLI 237,5–240; FI 89,5–92,1; SI 108,4–110,6; TI 45,1–48,2; PI 87,5–93,8.

Pale brick red to brownish all over, except the eyes and abdomen which are black; the apical margins of the latter testaceous. In the darker specimens the coxae, apical half of the flagella, apical portions of the scapes and the cheeks somewhat darker in colour. Mandibular teeth blackish brown to brownish. Head and truncus fairly dull, the mandibles, clypeus and node a little more shining, legs and abdomen shining. Head, truncus and the node reticulate-rugulose, the fine rugae almost concentrically arranged on each side of the disc of the pronotum, semi-circularly on the mesonotum and transversely on the epinotum and petiole, obliquely so on the sides of the truncus. Mandibles finely longitudinally striolate and dull on the basal half, the sculpture effaced on the apical portion and more shining. Abdomen also finely reticulate-rugulose, the rugae transversely arranged, the sculpture stronger on the basal segment, becoming more superficial towards the apex. Legs and antennae microscopically rugulose, the scapes somewhat duller. *Pubescence* short, decumbent, yellowish, sparse, more abundant on the coxae and flagella, somewhat longer on the abdomen. *Pilosity* erect, long, yellowish, consisting of the following: a transverse row of about 8–9 on the anterior border, and 4 on the median area of the clypeus; 4 on the vertex; 2 on the occiput; 2 each on the pro- and mesonotum; 2 on the brow of the epinotum; 4 on the posterior side of the node, and two transverse rows on each abdominal segment, one in front of the apical margin and one of 4 setae in the middle; there are also some pilose hairs on the ventral side of the body.

Head nearly two-seventeenths to one-eleventh longer than wide and about one-fifth wider than the pronotum, the sides almost straight, the hind margin very convex, about as wide in front as behind, *frontal area* not very clearly

demarcated behind, *frontal sulcus* indicated by a thin, shining line. *Frontal carinae* sinuate, extending to the posterior two-fifths of the head, the distance between them behind being about equal to their length, the *eyes* occupying nearly three-tenths of the length of the head and situated behind the middle of the sides. *Clypeus* obtusely carinate on the posterior half, without lobe, the front margin convex. Mandibles triangular, projecting well in front of the head, with five sharp teeth, the apical one the largest, the basal and masticatory margins each with a row of long hairs. *Scapes* about as long as the head, extending beyond the hind margin by nearly three-eighths of their length; the flagellum almost two-fifths longer than the scape; all the joints longer than wide, the 2nd-10th about equal in length, the first joint as long as the apical and much longer than the rest.

Truncus about twice (or slightly more) as long as wide and nearly five-eighths wider over the pronotum than over the brow of the epinotum, the pro-mesonotal suture distinct, the *meso-epinotal suture* fairly well indicated, continuing on the sides as an oblique impression behind the meso-thoracic stigmata. In profile the pro-mesonotum forms a wide curve up to the meso-epinotal suture, behind this point the *epinotal dorsum* is very concave and saddle-shaped, forming a small prominence behind this suture on the median line and a high rounded brow at the back, the declivity oblique and about three-fifths the length of the dorsum, fairly shining and finely and transversely striolate; seen from above the floor of the epinotal concavity is flat and narrower in front than in the middle, the sides almost parallel. *Petiolear node* subglobose, very slightly longer than wide, seen in profile as high as wide, the dorsum slightly convex, the very short front and longer hind faces vertical, the ventral surface somewhat concave; its peduncle very short. *Abdomen* rounded at the base, the acidopore with a fringe of very short setae. *Legs* moderately long.

Type series: 2♂♂, South African Museum. Garies, Namaqualand, 5 October 1959 (A. J. Prins).

2 ♂♂, Plant Protection Research Institute, Pretoria. Same date and locality.

This species has also been collected near Bitterfontein, C.P., and near Hondeklip Bay, C.P., and I should not be surprised if it eventually is found to be distributed throughout Namaqualand and Great Namaland.

Camponotus sellidorsatus n.sp.

(Figs 25, 26, 34A, B)

♂ TL 5,0-5,4 mm; HL 0,96-1,02 mm; WL 1,30-1,32 mm; PL 0,24 mm; HFL 1,0-1,10 mm; MFL 0,82-0,90 mm; ED 0,66-0,72 mm; SL 0,88-0,94 mm; CL 0,28-0,30 mm; FL 0,68-0,72 mm; L 2,68-2,80 mm; CI 95,8-98,03; CTI 73,8-77,3; CLI 242,9-260; FI 97,1-100; SI 94-95,7; TI 53,8-56,1; PI 141,7.

Brownish black, the flagella, tarsi and mandibles more brownish, apical margins of abdominal segments and peduncle of the petiole paler or testaceous; basal margins of mandibles black, the teeth brownish red. Moderately shining, the legs and abdomen more shining than the rest, the hind part of the head duller; the mandibles very finely reticulate-striolate, the fine striae longitudinally arranged, and with large piliferous punctures, the anterior part of the mandibles fairly shining. Finely reticulate-rugulose all over, the fine rugae obliquely arranged on the sides of the truncus; transversely so on the epinotum and nodes; the antennae and legs microscopically reticulate-rugulose. *Pubescence* and *pilosity* as in *namacolus*, although there seem to be four setae on the occiput and on the brow of the epinotum.

Head very slightly longer than wide and about two-ninths to almost one-fourth wider than the truncus, the sides a little convex, narrower in front than in the middle, the hind margin as convex as in *namacolus*, the *frontal area* more clearly marked, the *frontal carinae* as in that species, the *frontal sulcus* somewhat more distinct. The *eyes* oval, occupying about three-tenths of the length of the head and situated behind the middle of the sides. The *clypeus* as in *namacolus*. The *scapes* slightly shorter than the head, extending beyond the hind margin by almost one-third to two-fifths of their length, their bases widened and as wide here as their apices; the flagellum two-fifths (or slightly more) longer than the scape, all the joints longer than wide, the 2nd the shortest, the 3rd-10th equal in length, the 1st longer than the rest and about as long as the apical joint.

The *truncus* nearly twice as long as wide (or slightly less) and also about five-eighths wider over the pronotum than over the brow of the epinotum, the *mesoepinotal suture* obsolete above but indicated on each side by a triangular impression. In profile the mesonotum appears somewhat gibbous, the epinotal concavity being shorter than in *namacolus* and therefore deeper but almost as flat; the brow of the epinotum and its declivity similar to those of the latter species. *Petiolar node* about two-sevenths wider than long, seen from above the outline is oval, seen from the side as high as wide, the dorsal surface sloping forward, the short front and longer hind faces nearly vertical, the ventral surface almost straight, its peduncle short. *Abdomen* rounded at the base, the acidopore with a fringe of short setae as in the previous species. *Legs* moderately long, the hind legs shorter than in *namacolus*.

Type series: 1 ♂, South African Museum. Hondeklip Bay, Namaqualand, 8 January 1971 (A. J. Prins).

2 ♀♀, Plant Protection Research Institute, Pretoria. Same date and locality (in alcohol) (A. J. Prins).

The *Tetramorium*-like *namacolus* may easily be distinguished from *sellidorsatus* by the reddish head and truncus; the latter very closely resembles a cock-tail ant when moving slowly over the ground; both seem to have the same distribution although they have not yet been found together. I have placed these two species in the subgenus *Mayria* until more material is available for further study.

SUMMARY

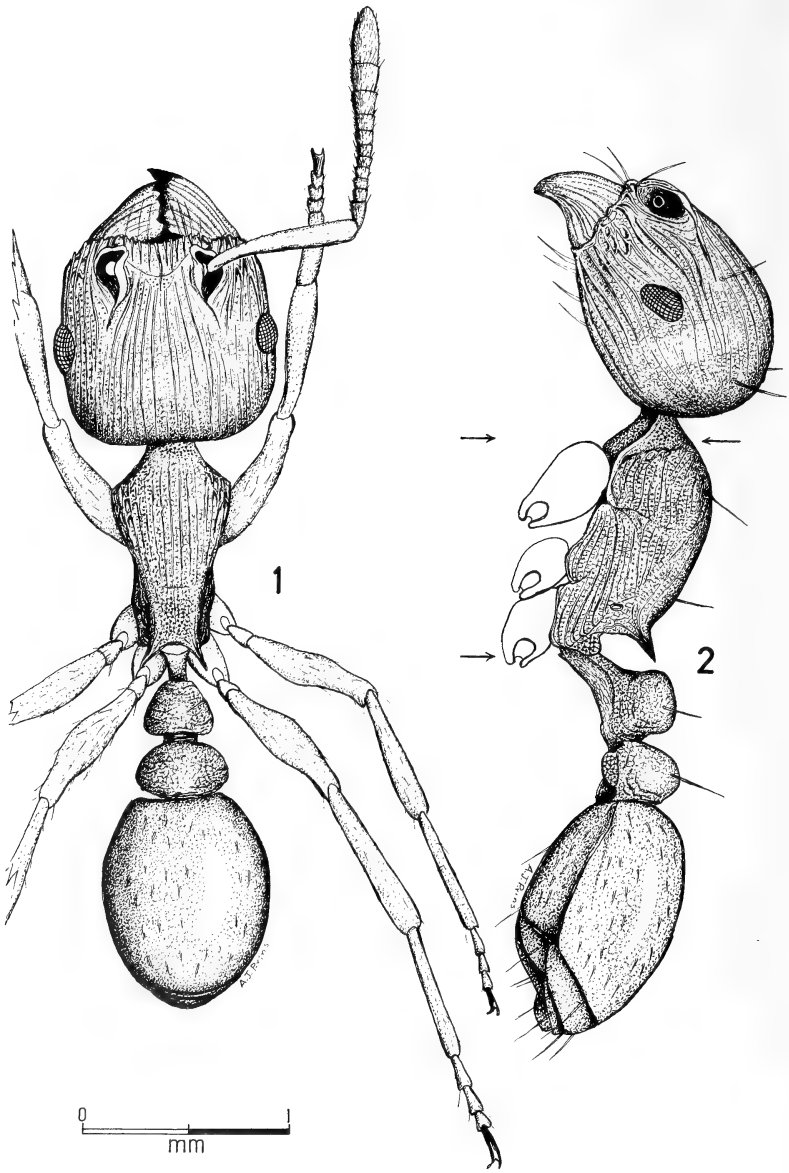
In this paper five types and 2 series of determined specimens have been redescribed, apart from the descriptions of four new species, together with the necessary illustrations and a proposed key for the identification of the ants belonging to the *solidum* group is added for the reader's convenience. *T. solidum* Emery var. *dichroum* Santschi is raised to a subspecies of *peringueyi* Arnold.

ACKNOWLEDGEMENTS

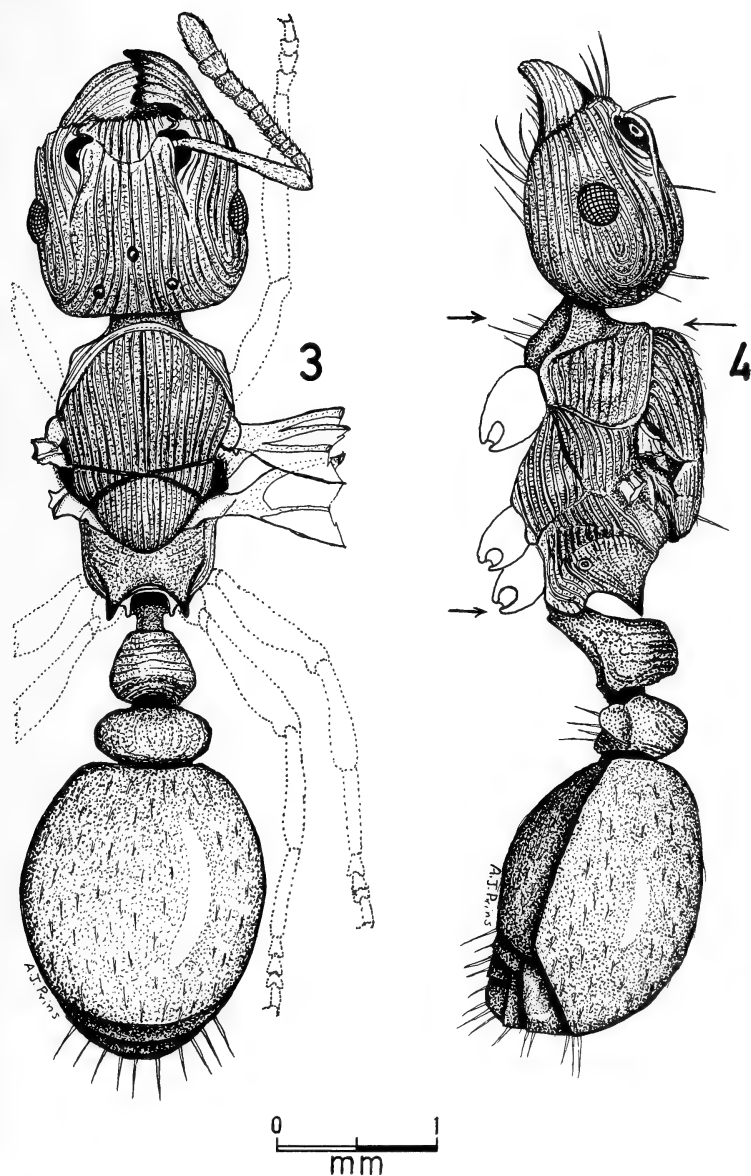
I am very grateful to Dr A. J. Hesse of this Museum for assisting me in the naming of the new species described here.

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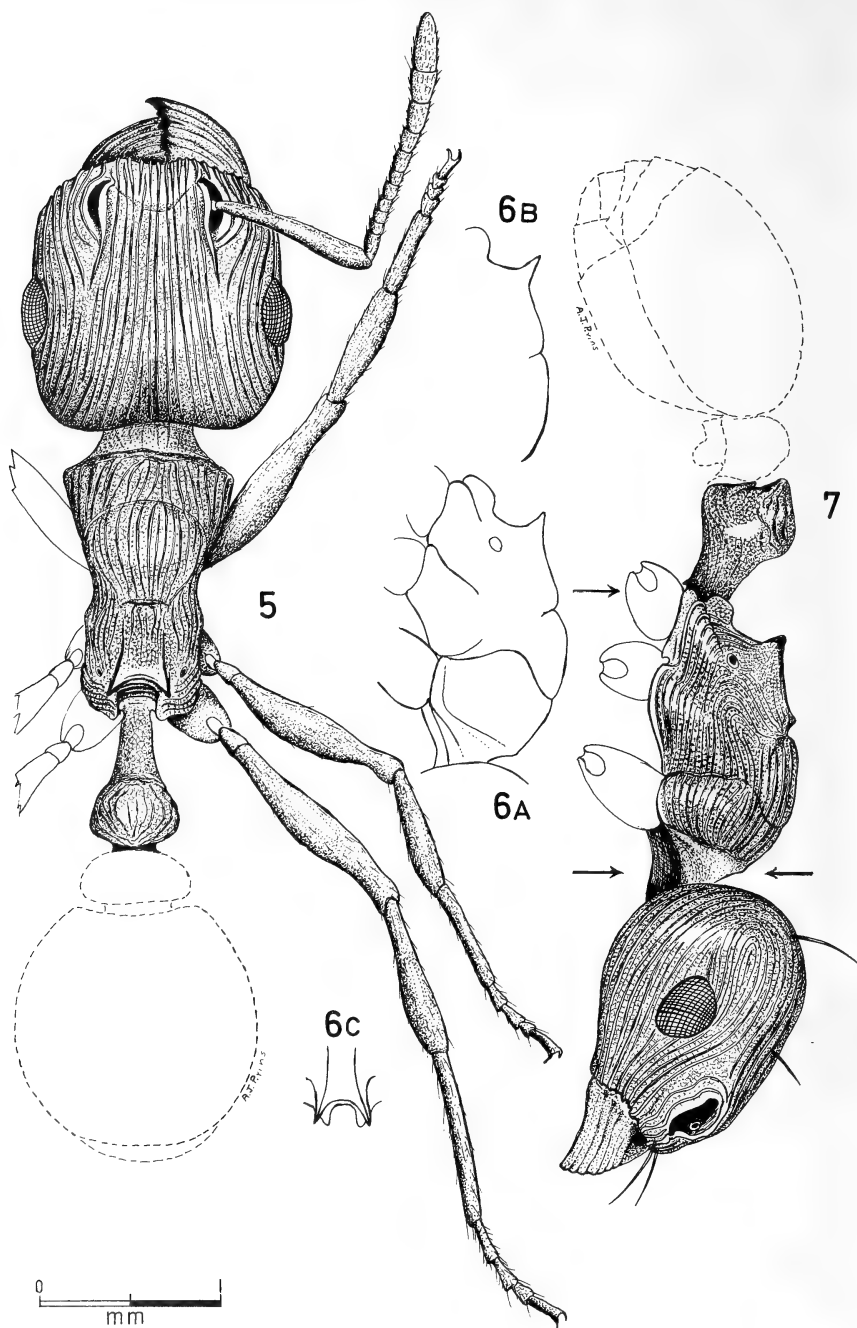
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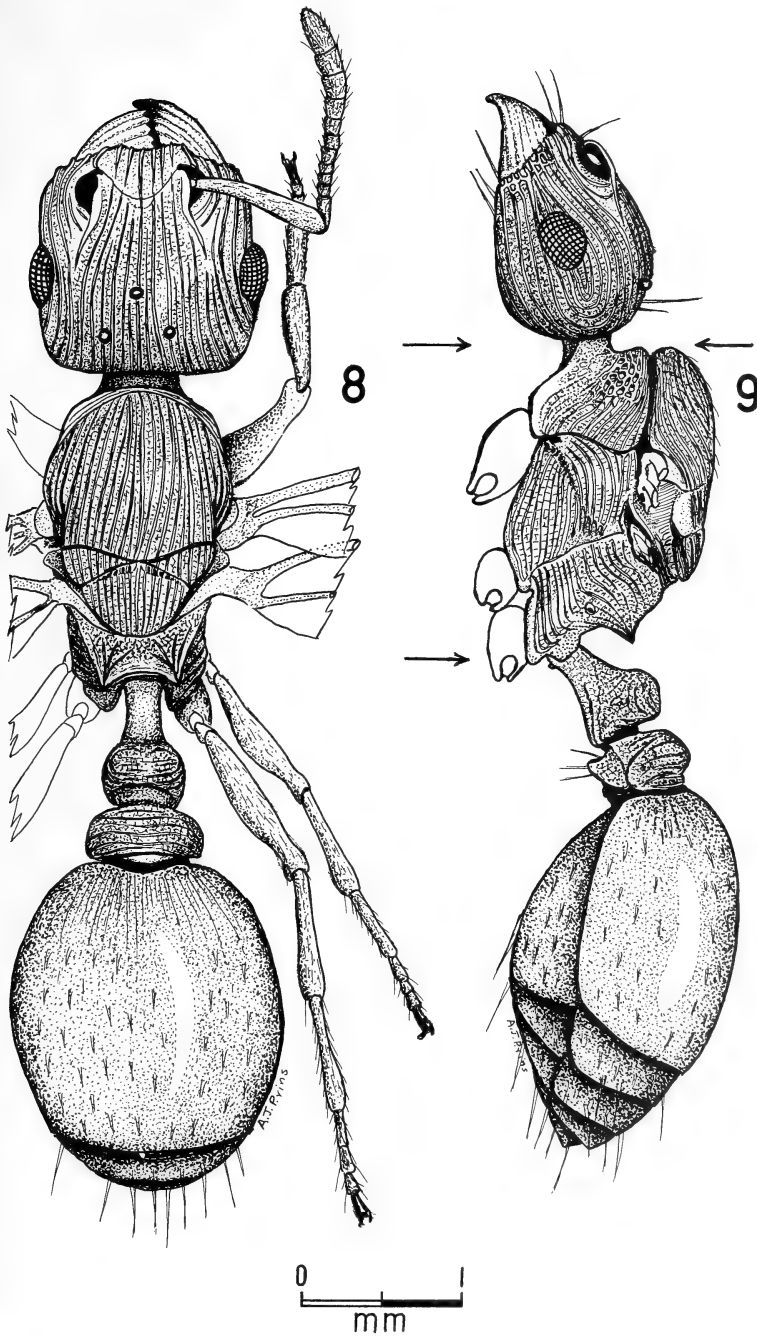
Figs 1-2. *Tetramorium solidum* Emery ♀.



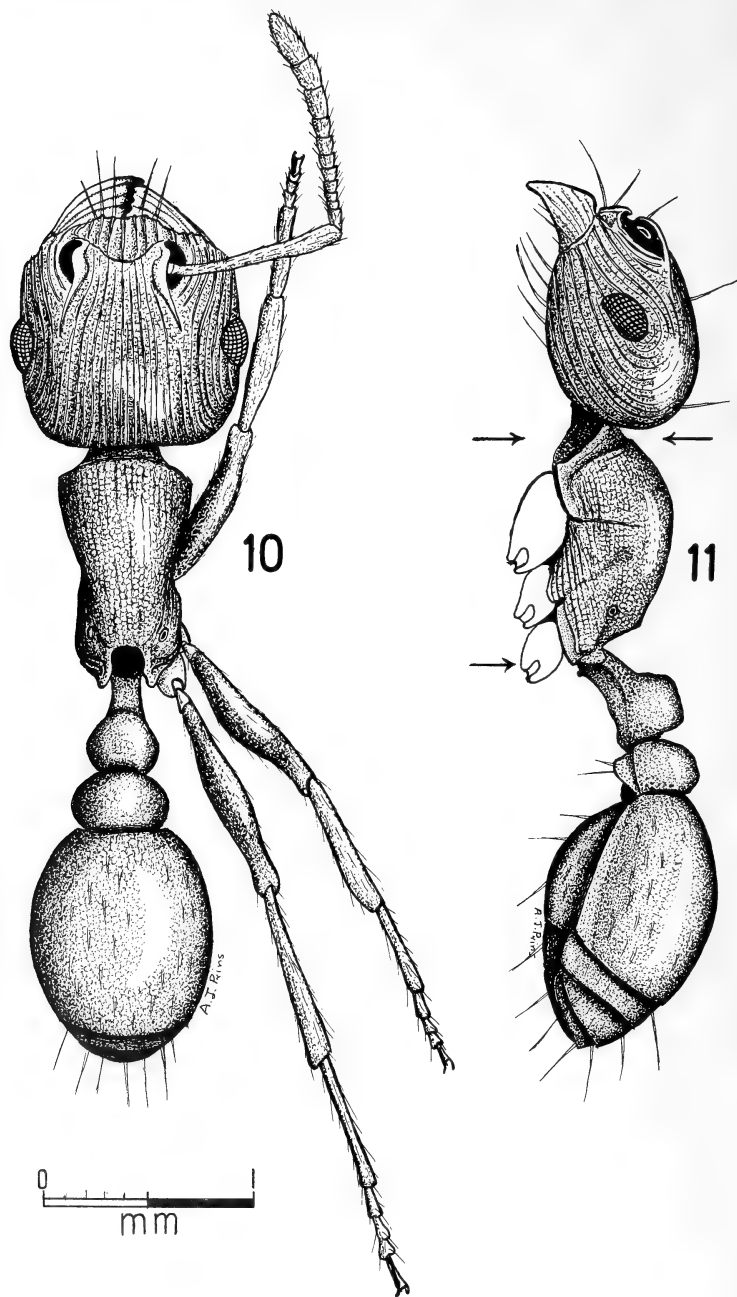
Figs 3-4. *Tetramorium solidum* Emery ♀.



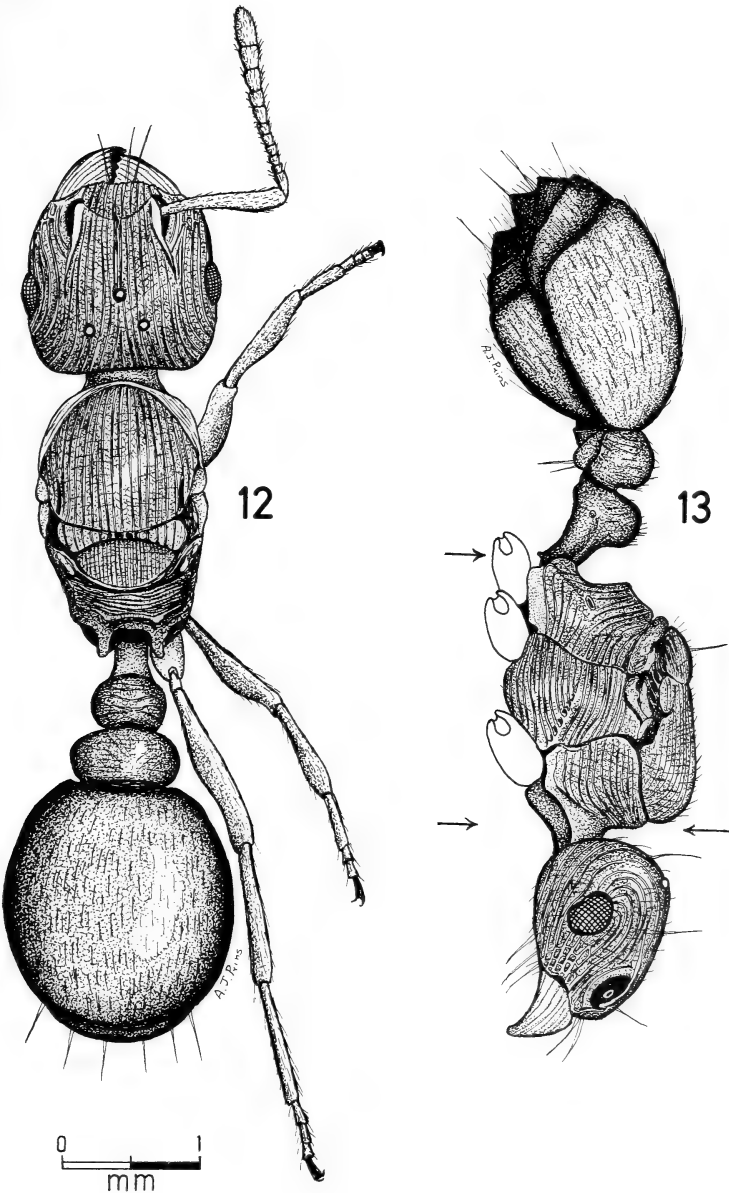
Figs 5-7. *Tetramorium solidum* Emery *tuckeri* Arnold ♀. 6A. Truncus of specimens from north-western Cape. 6B. Dorsal outline of truncus of specimens from South West Africa. 6C. Dorsal view of spines of specimens from South West Africa.



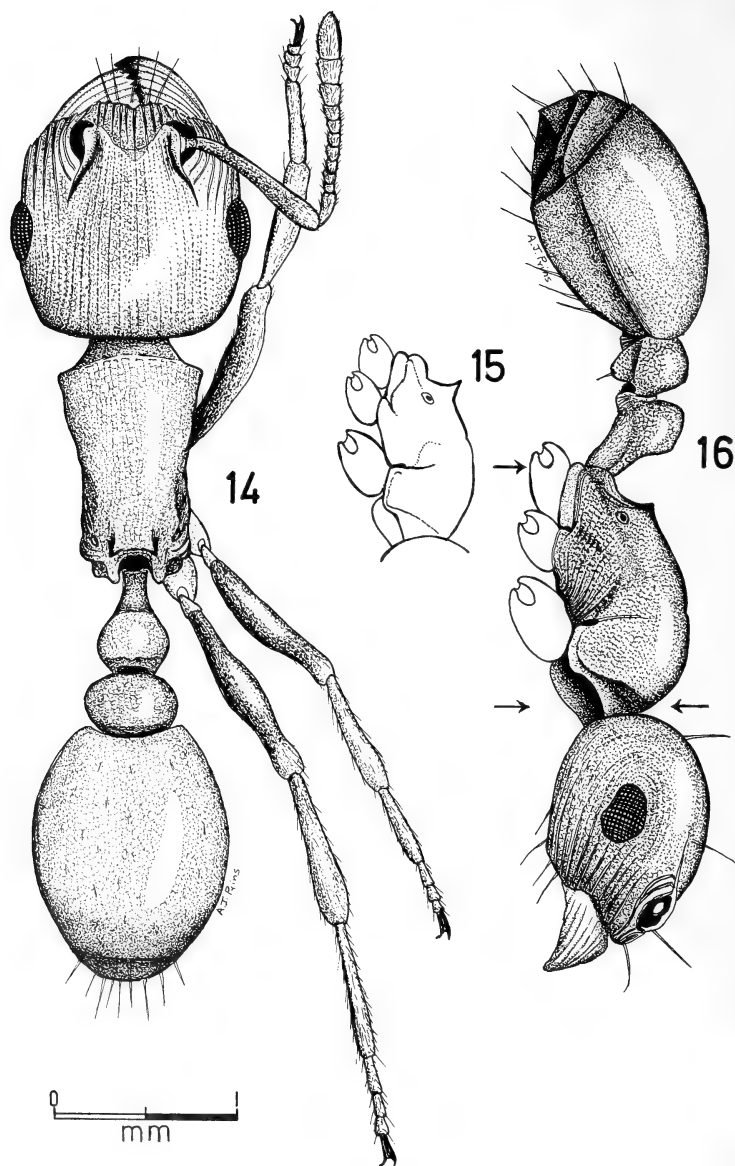
Figs 8-9. *Tetramorium solidum* Emery *tuckeri* Arnold ♀.



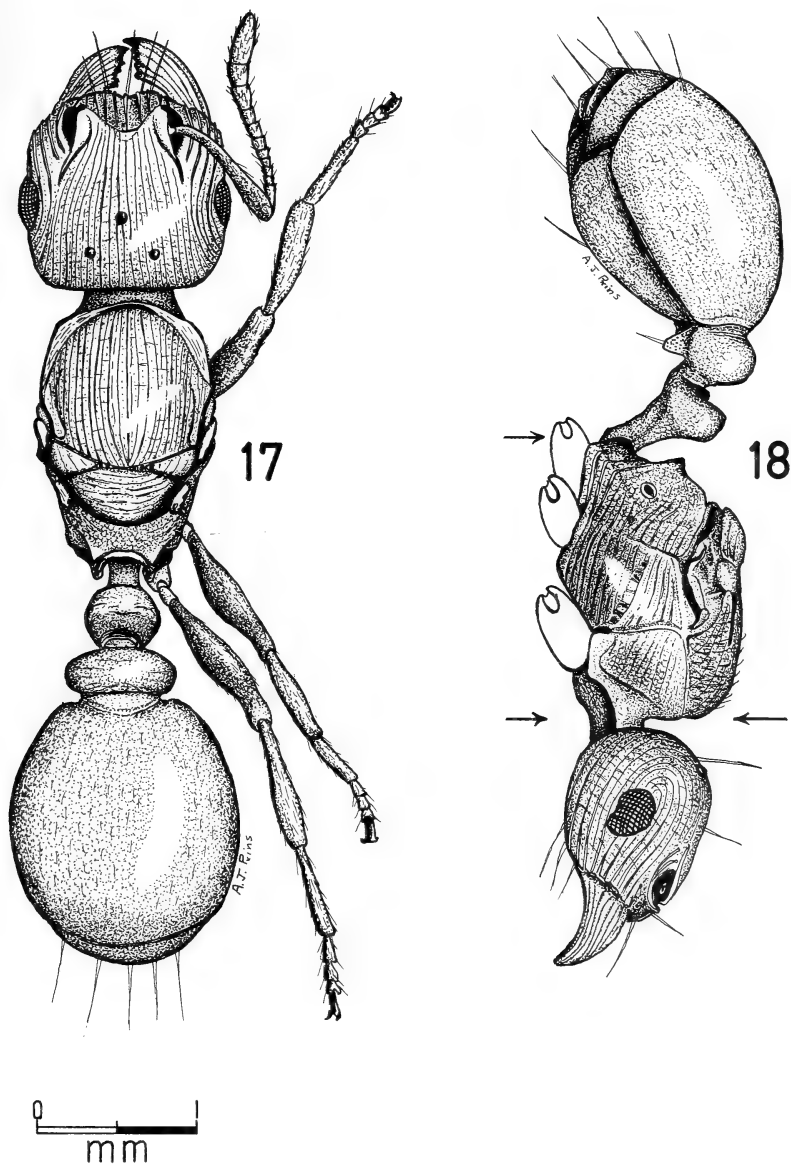
Figs 10-11. *Tetramorium aspinatum* n.sp. ♀.



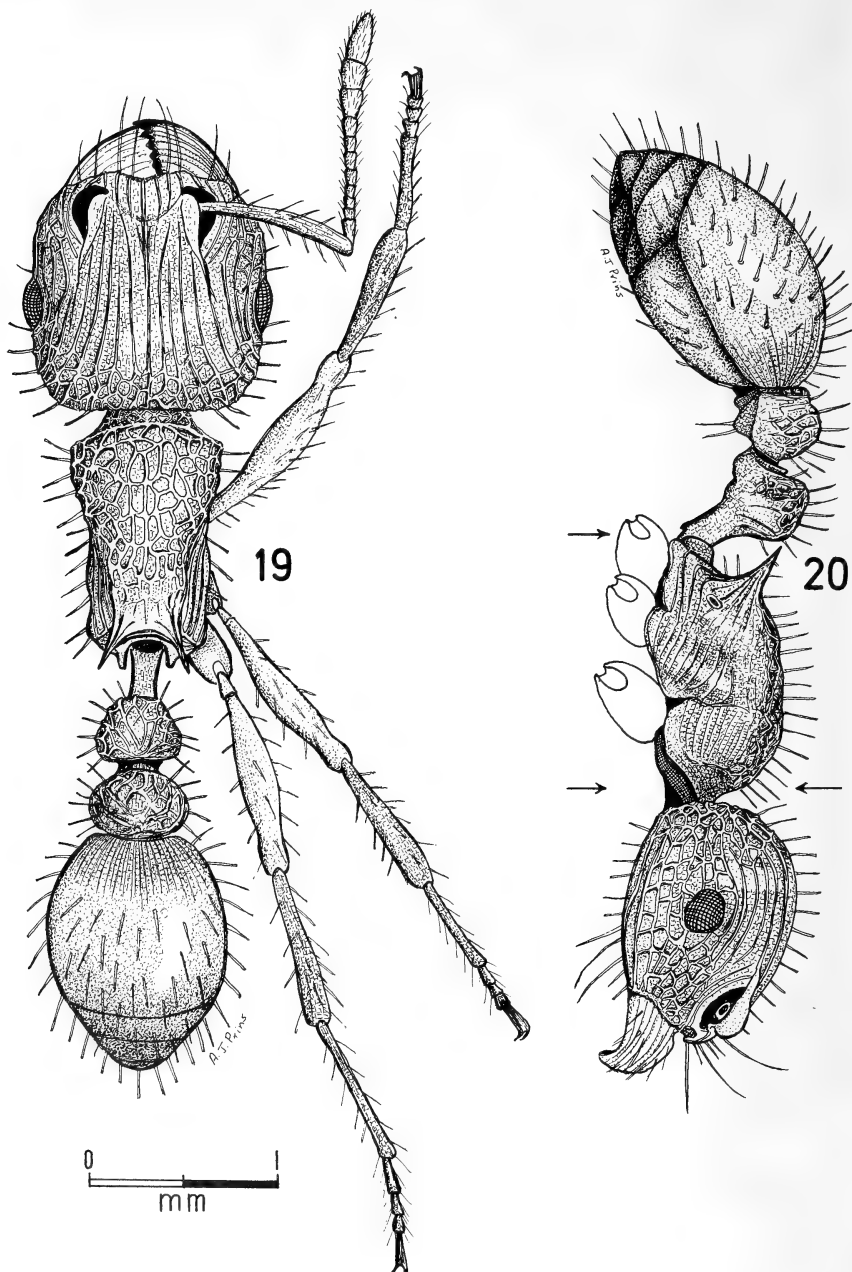
Figs 12-13. *Tetramorium aspinatum* n.sp. ♀.



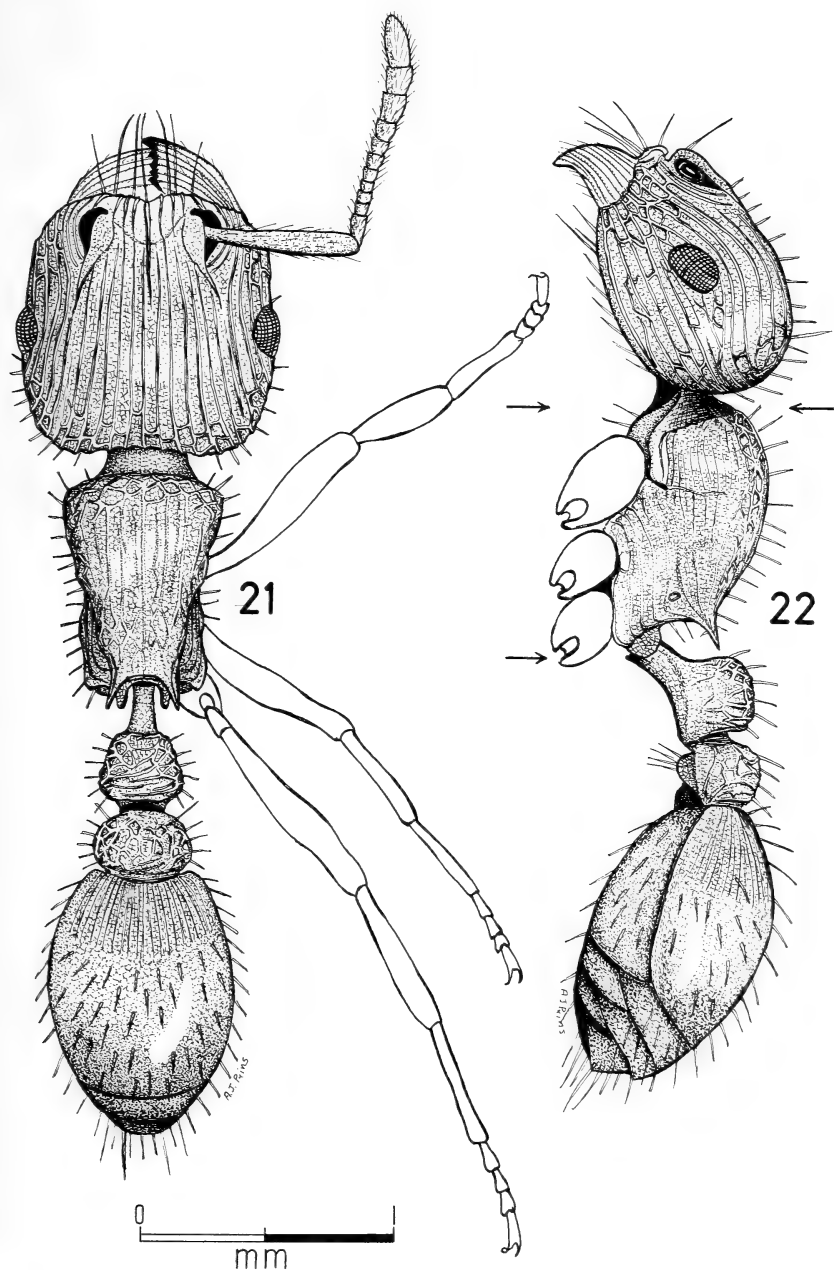
Figs 14-16. *Tetramorium rutilum* n.sp. ♀. 15. *Tetramorium rutilum*, smaller form, Vanrhynsdorp.



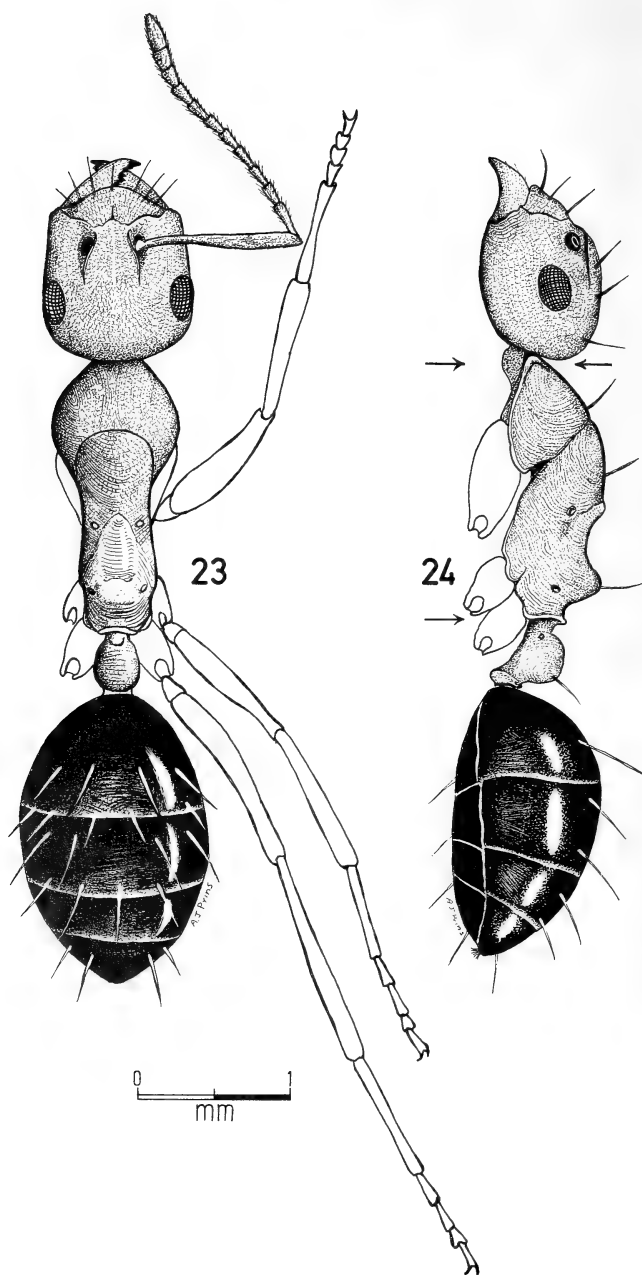
Figs 17-18. *Tetramorium rutilum* n.sp. ♀.



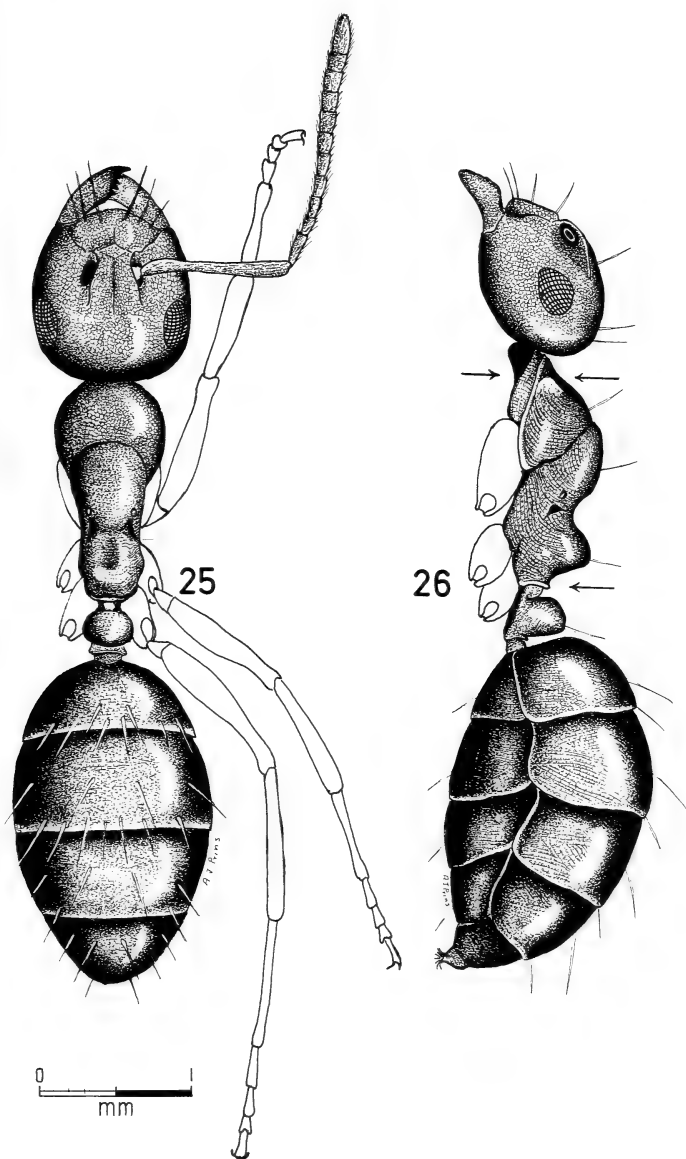
Figs 19-20. *Tetramorium peringueyi* Arnold ♀.



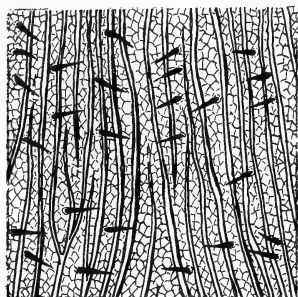
Figs 21-22. *Tetramorium peringueyi* Arnold *dichroum* Santschi ♀.



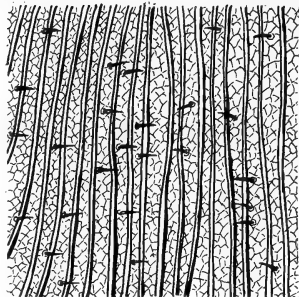
Figs 23-24. *Camponotus namacolus* n.sp. ♀.



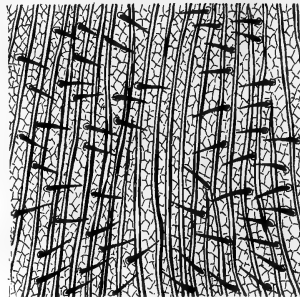
Figs 25-26. *Camponotus sellidorsatus* n.sp. ♀.



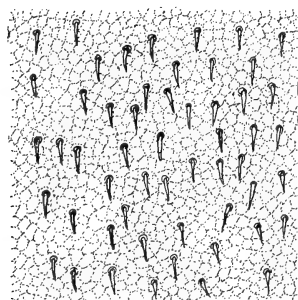
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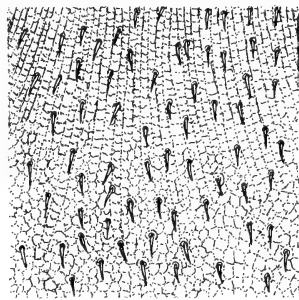
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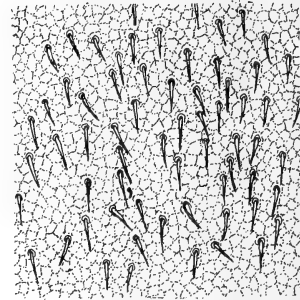
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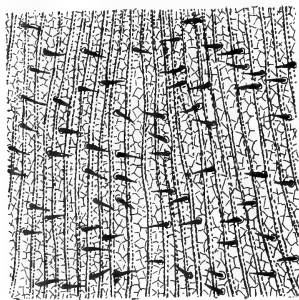
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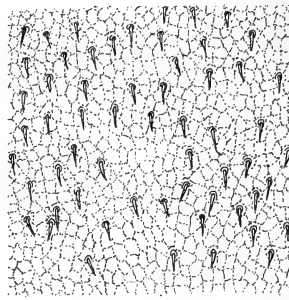
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29B

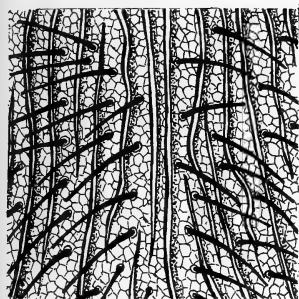


30A

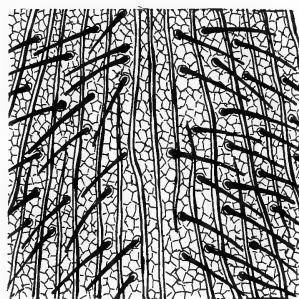


30B

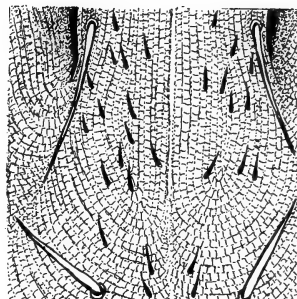
Figs 27-30. 0.5 mm² of (A) the vertex of the head and (B) the middle of the 1st abdominal segment to show the sculpture and the position of the setae. 27. *T. solidum* Emery; 28. *T. solidum* Emery *tuckeri* Arnold; 29. *T. aspinatum* n.sp.; 30. *T. rutilum* n.sp.



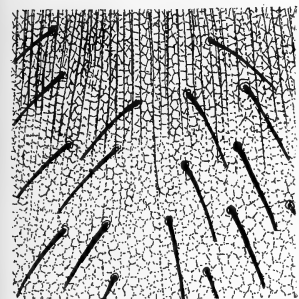
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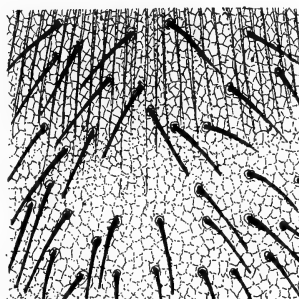
32A



33A



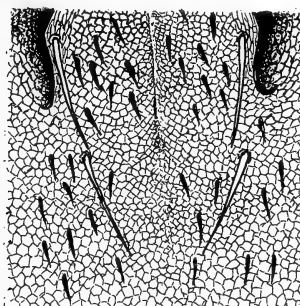
31B



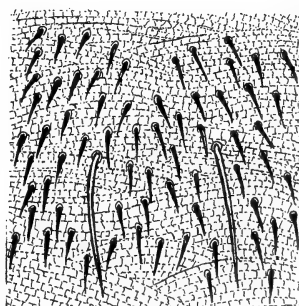
32B



33B

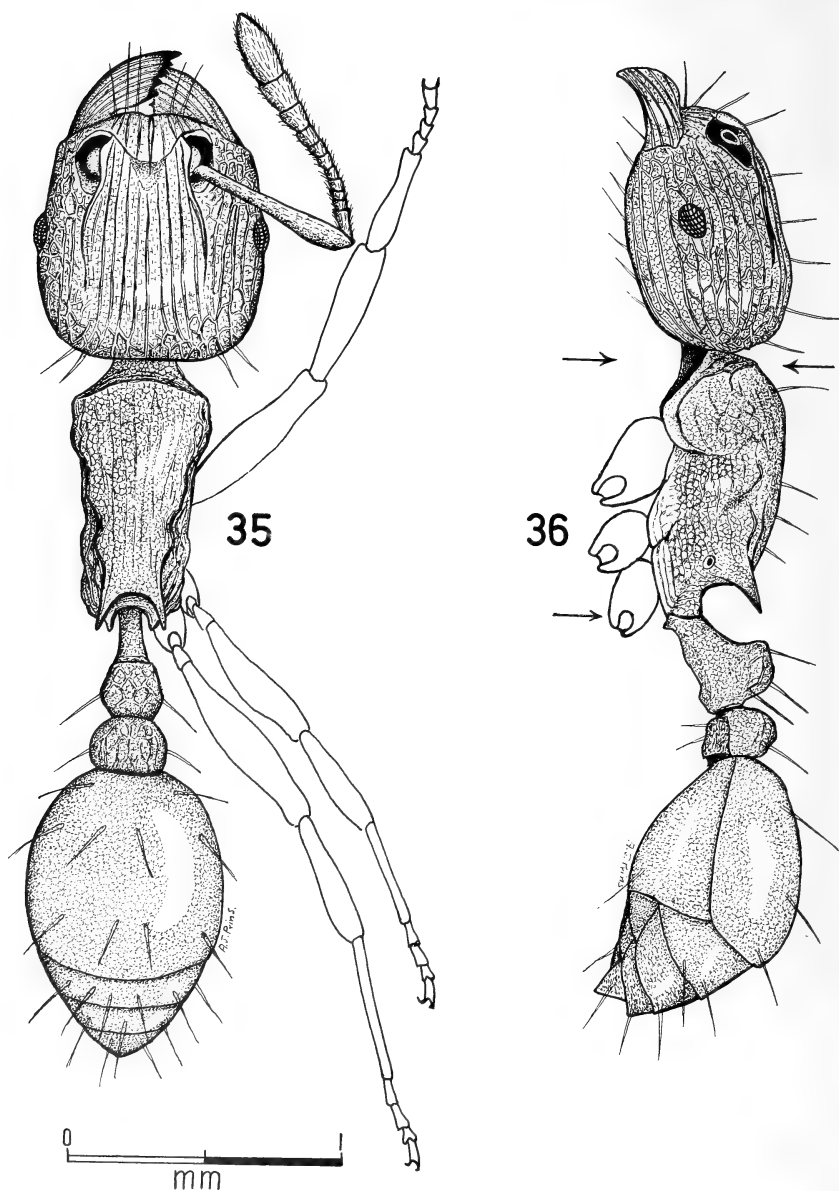


34A

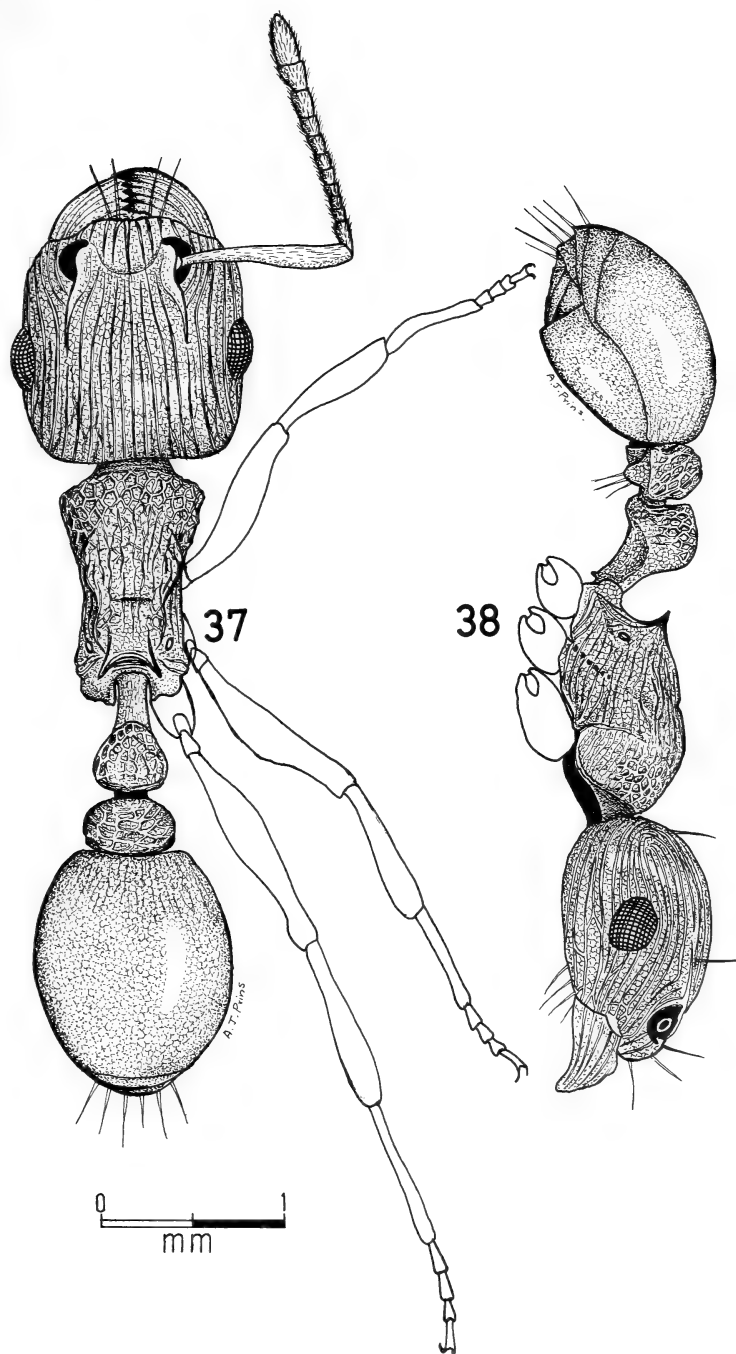


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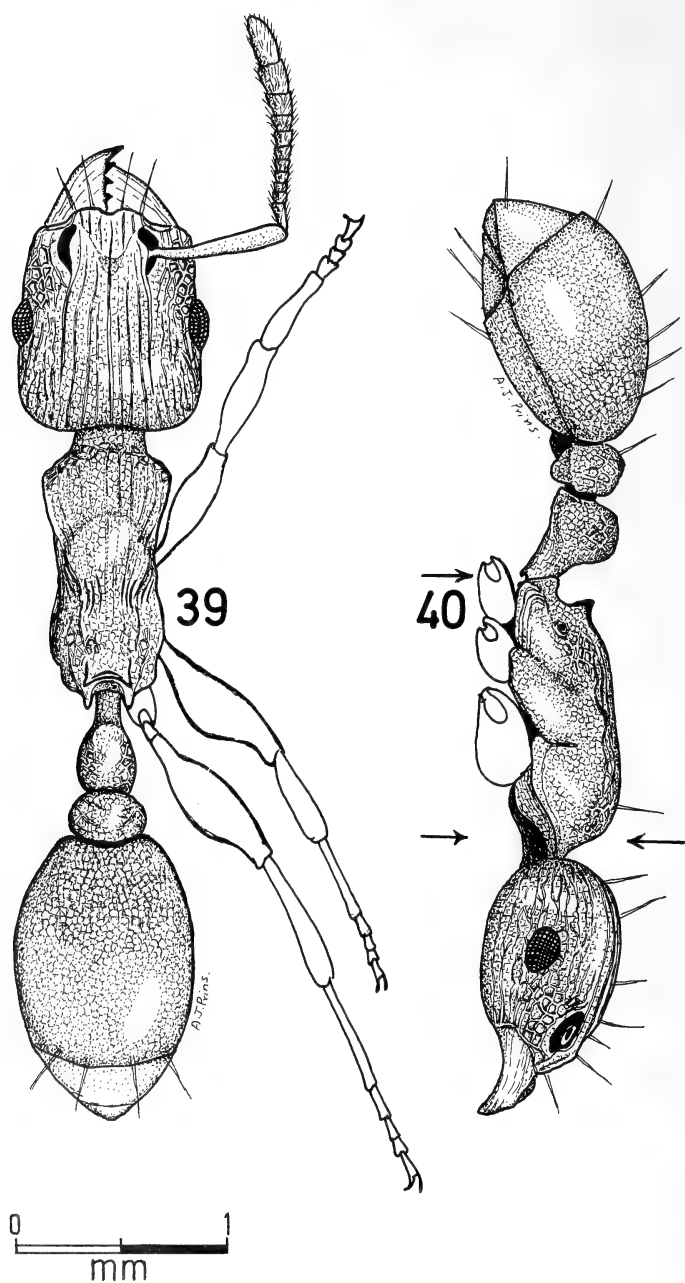
Figs 31-34. 0.5 mm² of (A) the vertex of the head and (B) the middle of the 1st abdominal segment to show the sculpture and the position of the setae. 31. *T. peringueyi* Arnold; 32. *T. peringueyi* Arnold *dichroum* Santschi; 33. *C. namacolus* n.sp.; 34. *C. sellidorsatus* n.sp.



Figs 35-36. *Tetramorium capense* Mayr ♀.



Figs 37-38. *Tetramorium solidum* Emery *signata* Emery ♀.



Figs 39-40. *Tetramorium jauresi* Forel ♀.

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KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309-320.

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THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika*. **4**: 269-270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269-270.

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THE SOUTH AFRICAN MUSEUM
DESCRIPTION OF FOUR NEW SPECIES AND
NOTES ON *TETRAMORIUM* MAYR

ANNALS

OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN





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CENOMANIAN AMMONITES
FROM NOVO REDONDO, ANGOLA

By
MICHAEL R. COOPER

Cape Town Kaapstad

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(With 13 figures)

[Ms. accepted 11 December 1972]

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INTRODUCTION

No previous ammonite faunas have been recorded from Novo Redondo (Fig. 1), although Thiele (1933) mentioned an *Acanthoceras* sp. and the Turonian *Mammites conciliatus* (Stoliczka) from this area. The latter was probably a mis-identification of the Middle Cenomanian *Euomphaloceras cunningtoni*, the outer whorls of which take on a mammitid appearance.

Beside the well-known Upper Cenomanian locality at Salinas, few undoubted Cenomanian ammonites have been recorded from Angola. Haas (1942) described a worn *Mantelliceras*? sp., together with the new species *Sharpeiceras goliath*, from north of Cabiri. Kennedy (1971: 66) considers the latter species '... is probably not separable from *S. laticlavum*'. An unsuccessful attempt was made to locate the collecting site mentioned by Haas, but no ammonites were found. Haughton (1925: 271) referred to a *Mantelliceras* sp., SAM 6728, herein confirmed and considered to represent *M. cf. saxbii* (Sharpe), from south of Porto Amboim.

All catalogue numbers refer to the collections housed in the South African Museum. Measurement abbreviations are as follows—D, diameter; H, height, i.e. distance from umbilical seam to venter; Hi, intercostal height; Hc, costal height; Wi, intercostal width; Wc, costal width; Ui, diameter of umbilicus between umbilical seams; Uo, diameter of umbilicus between umbilical bullae; T, thickness, i.e. distance from venter of penultimate whorl to venter of final whorl. All measurements are in millimetres.

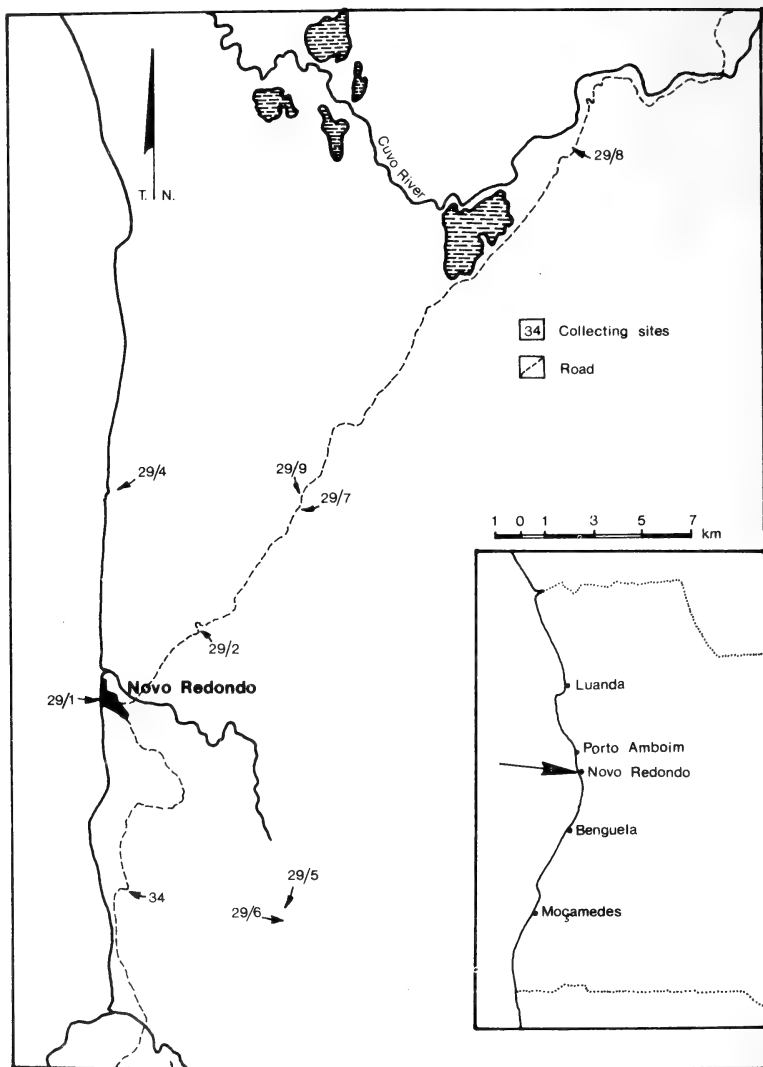


Fig. 1. Locality map.

GEOLOGY

Post-Cretaceous folding and faulting has tended to obscure the geological relationships, but the following very broad geological sequence is apparent.

Cretaceous strata extend as far east as the Cuvo River falls, where pale, unfossiliferous silts lie directly on Basement rocks. These are followed by thin, white, extremely hard, lacustrine limestones with fresh-water molluscs (Loc. 29/8). The succeeding pale silts are overlain by gypsiferous beds. Somewhat higher up, the first marine fossils occur in sandy limestones and silts, with

the appearance of *Neithea tricostrata* (Coquand), '*Trigonia*' sp., other bivalves, gastropods, echinoids, and the ammonite *Mantelliceras*. These beds (Loc. 29/7) are of Lower Cenomanian age. Closer to Novo Redondo (Loc. 29/2) higher beds of grey, coarse-grained calcareous sandstones and grits are entirely lacking in fossils. At Novo Redondo, dark grey shales, from a trench being excavated around the perimeter of the chapel, yielded crushed specimens of *Turrilites costatus* Lamarck and *Anisoceras plicatile* (J. Sowerby), together with indeterminate acanthostrate fragments. Somewhat higher beds, exposed both to the north (Loc. 29/4) and to the south (Loc. 29/6 & 34) of the town, contain a fauna rich in echinoids and the ammonites *Turrilites acutus* Passy, *Euomphaloceras cunningtoni* (Sharpe) and *Forbesiceras obtectum* (Sharpe). Bivalves and gastropods are uncommon.

SYSTEMATICS

Order AMMONOIDEA Zittel, 1884

Suborder **LYTOCERATINA** Hyatt, 1889

Superfamily TURRILITACEAE Meek, 1876

Family **Hamitidae** Hyatt, 1900

Genus STOMOHAMITES Breistroffer, 1940

Type species: *Hamites virgulatus* Brongniart, 1822

Stomohamites aff. *simplex* (d'Orbigny)

Fig. 2E

aff. *Hamites simplex* d'Orbigny, 1842: 550, pl. 134, figs 12-14.

aff. *Stomohamites simplex* (d'Orbigny) Kennedy, 1971: 6, pl. 1, figs 1-8.

Description

A single, poorly-preserved hamitid, SAM K2703, appears to be related to d'Orbigny's species, mainly by virtue of their equivalent ages in the Middle Cenomanian, *S. duplicatus* (Pictet & Campiche) being a Lower Cenomanian form.

The whorl section of the Angolan specimen is unknown, but would appear to be circular. Ornament consists of radial annular ribs of which there are about seven in a distance of 5 mm, a distance approximately equal to the diameter.

Discussion

The unique Angolan specimen differs from *S. simplex* in its apparently finer ribbing, and is thus closer to the *Hamites simplex* figured by Collignon (1928: 55, pl. 7, figs 1-3), which Sornay (1956) and Kennedy (1971) consider to belong to another species.

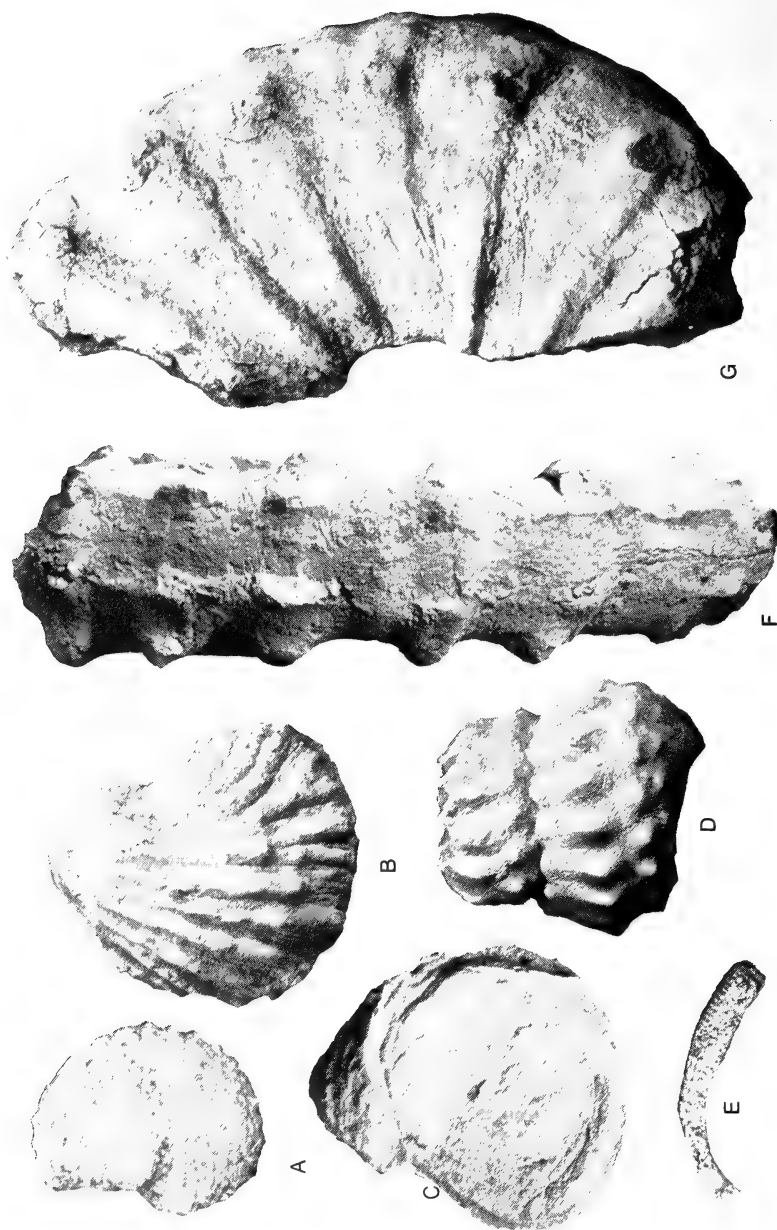


Fig. 2

A. *Forbesiceras obiectum* (Sharpe). Lateral view of poorly preserved nucleus, SAM K2700. Loc. 29/4. $\times 2$. B-C. *Exogyra* sp. Left and right valves of SAM K2577. Loc. 29/6. $\times 1$. D. *Turritites* (*Turritites*) *acutus* Passy. SAM K4126; lower row of tubercles concealed. Loc. 34. $\times 1$. E. *Stomohamites* aff. *simplex* (d'Orbigny). SAM K2703. Loc. 29/4. $\times 1$. F-G. *Acanthoceras* cf. *tunetana* Pervinquière. Ventral and lateral views of SAM K2928. Loc. 29/5. $\times 2/3$.

Family **Anisoceratidae** Hyatt, 1900Genus **ANISOCERAS** Pictet, 1854Type species: *Ammonites saussureanus* Pictet, 1847*Anisoceras plicatile* (J. Sowerby)

Fig. 3D

Hamites plicatilis J. Sowerby, 1819: 281, pl. 234, fig. 1.*Anisoceras plicatile* (J. Sowerby) Kennedy, 1971: 12, pl. 3, figs 12, 13; pl. 4, figs 1-3.*Description*

A single very crushed specimen, SAM K3545, is assigned to this genus by virtue of the association of two lateral ribs per ventro-lateral tubercle. It is preserved as a composite internal mould in shale.

The shell has a typical *Anisoceras* form and is loosely coiled in a single (?) plane. The whorl section is unknown. The ornament consists of rather dense, fine, flexuous, distinctly rursiradiate ribbing, narrower than the interspaces which are about 3 mm wide. There are septate spines high up on the flank, with each of which are associated two flank ribs. There are generally two ribs between each spine. The nature of the venter is unknown.

Discussion

The apparent lack of lateral tubercles, possibly due to crushing, makes its assignation to *Anisoceras* somewhat tentative. In all other respects, however, the ornament closely resembles *Anisoceras plicatile* which, according to Kennedy (1971: 13) '... is frequent in the lower part of the *rhodomagense* Zone'.

Family **Turrilitidae** Meek, 1876Genus **TURRILITES** Lamarck, 1801Type species: *Turrilites costatus* Lamarck, 1801*Turrilites* (*Turrilites*) *costatus* Lamarck

Fig. 3E

Turrilites costata Lamarck, 1801: 102.*Turrilites* (*Turrilites*) *costatus* Lamarck, Clarke, 1965: 53, figs 20a, b; pl. 20, figs 1, 2, 7, 8.

Kennedy, 1971: 30, pl. 6, fig. 3, pl. 8, figs 12-14.

Description

A number of crushed specimens, preserved as internal moulds, undoubtedly belong to this species, showing the characteristic development of ribs on the adapical portion of the outer whorl surface, which join the upper row of tubercles, the latter being bullate.

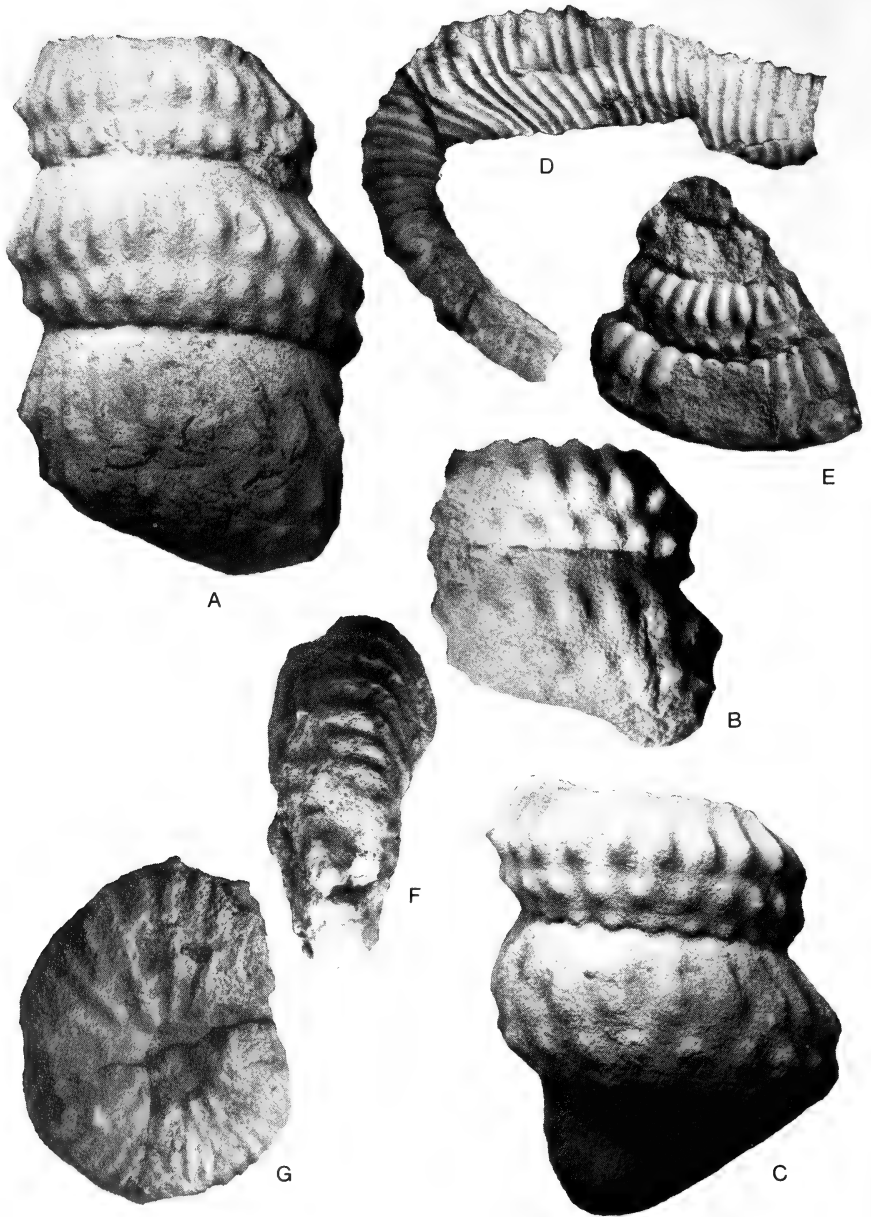


Fig. 3

A-C. *Turrilites* (*Turrilites*) *acutus* Passy. A. SAM K4101. $\times 2/3$. B. SAM K4103; lower row of tubercles concealed. $\times 1$. C. SAM K4100; lower row of tubercles exposed. $\times 2/3$. All from Loc. 29/6. D. *Anisoceras plicatile* (J. Sowerby). SAM K3545. Loc. 29/1 $\times 1$. E. *Turrilites* (*Turrilites*) *costatus* Lamarck. SAM K3540. Loc. 29/1. $\times 1$. F-G. *Mantelliceras* cf. *saxbii* (Sharpe). Ventral and lateral views of SAM 6728. $\times 1$.

Discussion

This species ranges from the top of the *Mantelliceras mantelli* zone, throughout the *rhotomagense* zone, attaining its greatest abundance at the base of the latter zone, where Kennedy (1971) has recognized a *Turrilites costatus* faunal assemblage.

Turrilites (Turrilites) acutus Passy

Figs 2D, 3A-C, 8D, 13B

Turrilites acutus Passy, 1832: 334; Diener, 1925: 79. Collignon, 1964: 53, fig. 1489. Clarke, 1965: 54, pl. 19, fig. 7. Kennedy, 1971: 30, pl. 7, figs 7, 8.

Turrilites dearingi Stephenson, 1952: 30, pl. 44, figs 6-8. Clarke, 1965: 55, pl. 20, fig. 4. Kennedy, 1971: 31.

Description

This well-known species is represented by numerous large examples from Novo Redondo, both with the lower row of tubercles exposed, as in *T. dearingi*, or concealed, as in *T. acutus*, indicating the two 'species' to represent nothing more than intra-specific variation.

The shell is spirally coiled, sinistral, with a very acute spiral angle. The whorls are in contact, with the outer face gently convex intercostally, but angular, polygonal in costal section.

The outer face is ornamented with three spiral rows of prominent tubercles, arranged on weak, oblique ribs, of which there are 19-20 per whorl. The upper tubercles are the most prominent and are somewhat bullate, lying slightly above mid-flank. The lower pair of tubercles are more conical, and not as prominently developed. The distance between the middle and upper row of tubercles is greater than that between the middle and lower row. The lowest row may be exposed (Fig. 3C), or concealed (Fig. 3B) by the succeeding whorl. The upper line of contact of each whorl is crenulated. The lower surface is gently convex and lacking in ornament. The upper whorl surface is strongly concave, with an acute shoulder. The suture-line is well preserved in some of the specimens (Fig. 4).

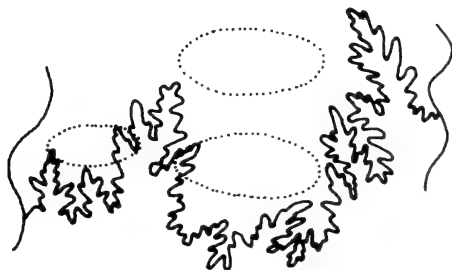


Fig. 4

Suture-line of *Turrilites acutus* Passy. $\times 2\frac{1}{2}$.

A single, aberrant specimen (Fig. 13B) develops a shallow spiral groove between the middle and upper row of tubercles, slightly above mid-flank, on the final two whorls, and is associated with the disappearance of the upper row of tubercles and a marked weakening of the lower two rows. Other specimens at similar, and larger, growth stages show no sign of this phenomenon.

Discussion

Kennedy (1971: 31) pointed out that the only difference between *T. acutus* and *T. dearingi* was that the lower row of tubercles was exposed on the outer flanks of the whorls of the latter species, and concluded that this species '... may merely be an aberrant *T. acutus*'. Whilst the Angolan material shows *T. (Turrilites) dearingi* not to be aberrant, it must be considered to fall within the intra-specific limits of *T. acutus*. From the Angolan material it appears that the lower row of tubercles is covered during the early ontogenetic stages, becoming exposed with age.

Superfamily DESMOCERATACEAE Zittel, 1895

Family **Desmoceratidae** Zittel, 1895

Subfamily **Puzosiinae** Spath, 1922

Genus PUZOSIA Bayle, 1878

Type species: *Ammonites subplanulatus* Schlüter, 1871

?*Puzosia* sp. indet.

Description

A puzosiid fragment is referable to either this genus or *Austiniceras*. The specimen is moderately large, with an evenly-arched venter and slightly convex flanks, which converge towards the venter. The venter is ornamented with distinct, narrow, prorsiradiate ribs which form a chevron across the venter. There are six ribs within a 15 mm distance along the venter.

Superfamily ACANTHOCERATACEAE Hyatt, 1900

Family **Lyelliceratidae** Spath, 1921

Subfamily **Forbesiceratinae** Wright, 1952

Genus FORBESICERAS Kossinat, 1897

Type species: *Ammonites largilliertianus* d'Orbigny, 1841

Forbesiceras obtectum (Sharpe)

Figs 5, 6A-B

Ammonites obtectus Sharpe, 1853: 20, pl. 7, figs 4a-c.

Forbesiceras obtectum (Sharpe) Kennedy, 1971: 47, pl. 16, fig. 3; pl. 9, figs 3a, b; pl. 46, fig. 3

Description

This species, together with *Turrilites acutus* Passy, forms the most abundant component of the Novo Redondo fauna and is represented by gigantic oxycones,

nearly all of which are, unfortunately, weathered composite internal moulds. Consequently, the ornament is known only from a single, small, specimen, SAM K2684. It is extremely involute and compressed, discoidal, with broad, slightly convex flanks. The very narrow venter is slightly convex, with a faint median keel. The ribbing is extremely faint, but is visible as strongly prorsiradiate striae on the inner half of the flanks. The outer half of the flanks shows rursiradiate ribbing projecting strongly backwards. The suture-line is well preserved in a number of specimens (Fig. 5).



Fig. 5

Suture-line showing first lateral saddle of *Forbesiceras obtectum* (Sharpe), SAM K2541. $\times 1$.

Measurements

No.		D.	H.	W.	T.
SAM K2684	..	118	79	28	?
SAM K2688	..	?	140	49	100
SAM K2691	..	305	?	± 60	?
SAM K2692	..	295	?	± 50	?
SAM K2687	..	195	± 120	42	± 90

Discussion

According to Kennedy (1971: 46) *Forbesiceras* is a medium-sized, rare ammonite genus. Neither of these statements is applicable to the Novo Redondo forms which are both extremely abundant and extremely large. Small nuclei of this genus (Fig. 2A), and presumably this species, occur at Locality 29/4 and show distinct ventro-lateral tubercles, with slightly prorsiradiate ribbing on the outer parts of the flank.



Fig. 6

A-B. *Forbesiceras obtectum* (Sharpe). Lateral and ventral views of SAM K2684. Loc. 29/6. $\times 1$.

Family **Acanthoceratidae** Hyatt, 1900Subfamily **Mantelliceratinae** Hyatt, 1900Genus **MANTELLICERAS** Hyatt, 1900Type species: *Ammonites mantelli* J. Sowerby, 1814*Mantelliceras* cf. *saxbii* (Sharpe)

Figs 3F-G; 7C-D

cf. *Ammonites saxbii* Sharpe, 1857: 45, pl. 20, figs 3a, b.cf. *Ammonites mantelli* Sharpe, 1857: 40, pl. 18, figs 4a, b only (*non* Sowerby).cf. *Ammonites feraudianus* Sharpe, 1857: 51, pl. 23, figs 6a-c (*non* d'Orbigny).cf. *Mantelliceras hyatti* Spath, 1925: 197.cf. *Mantelliceras ventnorense* Diener, 1925: 170. Kennedy, 1971: 62, pl. 26, figs 2a-c.*Description*

A single somewhat worn specimen, SAM K2506, was collected from the lowest fossiliferous marine horizon studied (Loc. 29/7). It is matched by an almost identical specimen, SAM 6728, from the 'sea-cliffs south of Benguela Velha (Porto Amboim)', discussed by Haughton (1925: 271) and now figured (Figs 3F-G).

The Novo Redondo specimen, SAM K2506, is preserved as a composite internal mould. The shell is compressed, with a whorl height: whorl width ratio of 1.25, and rather involute. The umbilicus is deep and fairly narrow, with a steep umbilical wall and a subrounded shoulder. The broad flat flanks converge slightly to the narrow, evenly-rounded venter. The ornament comprises alternating long and short prorsiradiate ribs, the former arising from small but distinct umbilical bullae. All ribs are ornamented with both upper and lower ventro-lateral tubercles. There are 15 ribs per half whorl, of which 7 are long ribs. The umbilical bullae extend on to the umbilical walls as radial primary ribs. The ribs pass straight up the flank to lower ventro-lateral tubercles, from which they bend sharply forwards to the upper ventro-lateral tubercles before joining across the venter. The latter is flat between the upper ventro-lateral tubercles.

Measurements

No.		D.	H.	Wi.	Wc.	Ui.	Uo.	T.
SAM K2506	..	40	20	16	?	9	15	?
SAM 6728	..	41	20	18	?	10	16	?

Discussion

Mantelliceras mantelli (J. Sowerby) differs from this species in being more inflated, with an octagonal whorl section, and in possessing mid-lateral tubercles. *Mantelliceras lymense* (Spath) is more finely ribbed than the Angolan example, with 25 ribs per half whorl, of which 7 are long ribs arising from



Fig. 7

A-B. *Calymenoceras caleroonense percostata* Collignon. Lateral and ventral views of SAM K2571. Loc. 29/6. $\times 1$. C-D. *Mantelliceras* cf. *saxbii* (Sharpe). Lateral and ventral views of SAM K2506. Loc. 29/7. $\times 1$.

umbilical bullae, whereas there are only 15 per half whorl in the Novo Redondo specimen. Kennedy & Hancock (1971) considered *M. ventnorense* Diener closely related to *M. saxbii*, and of doubtful specific status. This species has about 34 alternating long and short flexuous ribs per whorl, and is thus very close to the Angolan specimen. The ribbing in the latter is straight, however, and not flexuous.

The Angolan specimen bears a close resemblance to the holotype of *M. hyatti* Spath, considered a synonym of *M. saxbii* by Kennedy & Hancock (1971), but is more coarsely ribbed. The Isle of Wight specimen has 19 ribs per half whorl at a slightly larger diameter, of which 9 are long ribs. However, Houghton's example from Porto Amboim has a similar number of ribs, but appears to increase rather rapidly in inflation on the anterior portion of the outer whorl.

Genus CALYCOCERAS Hyatt, 1900

Type species: *Ammonites navicularis* Mantell, 1822

Calycoceras coleroonense percostata Collignon

Figs 7A–B

Calycoceras coleroonense Stoliczka var. *percostata* Collignon, 1964: 118, pl. 361, fig. 1584.

? *Calycoceras newboldi* var. *ankomakaensis* Collignon, 1937: 16, pl. 3, figs 7, 7a; pl. 8, fig. 6.

Collignon, 1964: 120, pl. 362, fig. 1588.

Description

Two slightly crushed specimens appear to belong to this subspecies. Both are preserved as composite internal moulds.

In SAM K2571, which has suffered slight lateral compression, the shell is compressed and evolute, with a wide, shallow umbilicus and a rounded umbilical shoulder. The flanks are almost flat and converge slightly to the evenly rounded venter. The outer whorl increases very slowly in height.

The ornament comprises rather dense, rounded, slightly flexuous ribs, generally alternating long and short, although occasionally there may be two short ribs intercalated between adjacent long ribs. The long ribs are ornamented with small but distinct umbilical bullae, while all ribs show the faintest hint of lower ventro-lateral swellings, and small, but distinct, upper ventro-lateral clavi. On the posterior portion of the outer whorl siphonal tubercles are very weakly developed. There are about 22 ribs per half whorl, 11 of which are long ribs. The greatest width is at the umbilical shoulder.

For comparative purposes measurements of other species are included below, with percentages in brackets.

Measurements

	No.		D.	H.	Wi.	Wc.	Ui.	Uo.	T.
SAM	K2571	..	94	35(37)	34(36)	35	?	52	?
	1	..	71	(41)	(42)	—	(35)	—	—
	2	..	61	(48)	(48)	—	(26)	—	—
	3	..	114	(39)	(43)	—	(32)	—	—
	4	..	105	(40)	(43)	—	(32)	—	—

The other species are as follows: 1 the type species of *C. newboldi ankoma-kaensis*; 2 the specimen figured by Collignon (1964); 3 the type species of *C. coleroonense percostata*; 4 the type species of *C. sinuosum*.

Discussion

Calycoceras coleroonense (Stoliczka) has flat flanks, with 25–35 ribs per whorl, and a sulcate venter in mature forms, although Stoliczka (1861: 71) considered the ‘. . . chief distinctive character of this species lies in the very gradual increase of the whorls in height and in the septa’. The Angolan form does not have a concave venter, while the ribbing is denser.

Calycoceras coleroonense percostata Collignon was erected for a more densely ribbed variety with 45 ribs per whorl, in which the venter was only very slightly concave, a feature not apparent in the figure. There appears no difference whereby the Angolan form can be separated from this subspecies.

Calycoceras sinuosum Collignon has the same general form as *C. coleroonense percostata*, indeed the measurements are virtually identical, with about 42 ribs per whorl, but apparently has finer, more flexuous ribbing. The differences are slight.

Calycoceras newboldi newboldi (Kossmat) is more inflated, with a narrower umbilicus, fewer, stronger ribs, and more prominent tuberculation. *Calycoceras newboldi ankomaensis* Collignon differs from the type in having flatter flanks, more evolute coiling, more ribs (42), higher whorls, and weaker tuberculation. It thus closely approaches *C. coleroonense percostata*. A comparison of the dimensions of these two forms shows that the type of *C. newboldi ankomaensis* is transitional between the smaller example figured by Collignon (1964: 120, pl. 362, fig. 1588) and the larger holotype of *C. coleroonense percostata*. It seems possible that the differences in the Madagascan species are due to comparison of different ontogenetic stages.

Calycoceras annulatum Collignon

Figs 8A–C

Calycoceras annulatum Collignon, 1964: 127, pl. 366, figs 1597, 1598.

Description

Two fragments of the outer whorls of rather large forms are assigned to this species, both preserved as composite internal moulds.

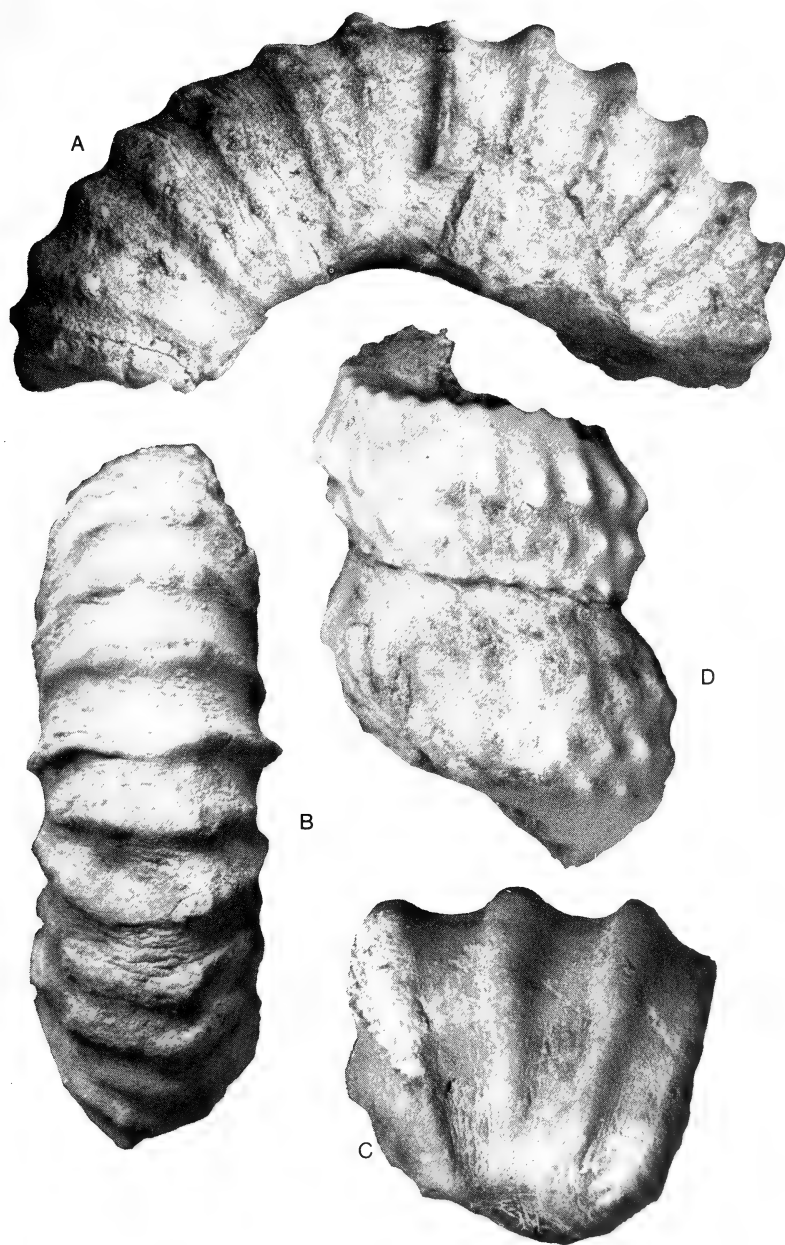


Fig. 8

A-C. *Calycoceras annulatum* Collignon. A-B, lateral and ventral views of SAM K2559. $\times 2/3$. C, lateral view of SAM K2580. $\times 2/3$. Both from Loc. 29/6.
 D. *Turrilites* (*Turrilites*) *acutus* Passy. SAM K2568. Loc. 29/6. $\times 2/3$.

In SAM K2559 the whorl section is slightly compressed, oval intercostally and with an angular, polygonal costal section. The umbilicus was wide and probably rather shallow, with sloping umbilical walls and an evenly-rounded umbilical shoulder. The flanks are convex and converge towards the rounded venter. Ornament comprises long and short ribs, which do not alternate. Thus, while 7 ribs arise at the umbilical shoulder only 10 cross the venter. The long ribs are ornamented with weak, strongly bullate umbilical tubercles, while all ribs have rather weak lower ventro-lateral tubercles and more prominent upper ventro-lateral tubercles. The ventro-lateral tubercles are also bullate due to the peculiar nature of the ribbing. The ribs are radial and very strongly flared, especially across the venter where the interspaces are strongly concave. Across the venter the costal section is slightly concave between the upper ventro-lateral tubercles. There is no sign of siphonal tubercles.

SAM K2580, which represents a much larger, still septate, growth stage and presumably belongs to this species, has fewer flared ribs, whilst also showing the faintest sign of siphonal clavi.

Measurements

No.	D.	Hi.	Hc.	Wi.	Wc.	Ui.	Uo.	T.
SAM K2559	± 140	42	45	39	42	± 53	?	?
SAM K2580	?	48	52	43	± 48	?	?	?

Discussion

The distant, prominently flared, ribbing of this species, recorded from the 'Lower Cenomanian' Zone à *Mantelliceras mantelli* et *Calycoceras newboldi* of Madagascar, is distinctive. The relation between this large species and the small *Calycoceras paucinodatum* (Crick), also associated with *Turrilites acutus*, requires looking into, especially in view of '... the considerable range of variation admitted in this species (*C. paucinodatum*)' by Kennedy (1971: 77).

Genus EUCALYCOCERAS Spath, 1923

Type species: *Ammonites pentagonus* Jukes-Browne, 1896

Eucalycoceras sp.

Figs 9C-D; 10C-D

Description

Two very worn fragments belong to this genus. Both are preserved as composite internal moulds.

The first example, SAM K2593, is a distinctly compressed form, with convex sides, converging slightly to the flattish venter. The maximum width is at the umbilical shoulder. Sinuous, slightly prorsiradiate long ribs arise either singly or in pairs from weak umbilical bullae. There is invariably one, occasionally two, shorter intercalated ribs between adjacent long ribs. There

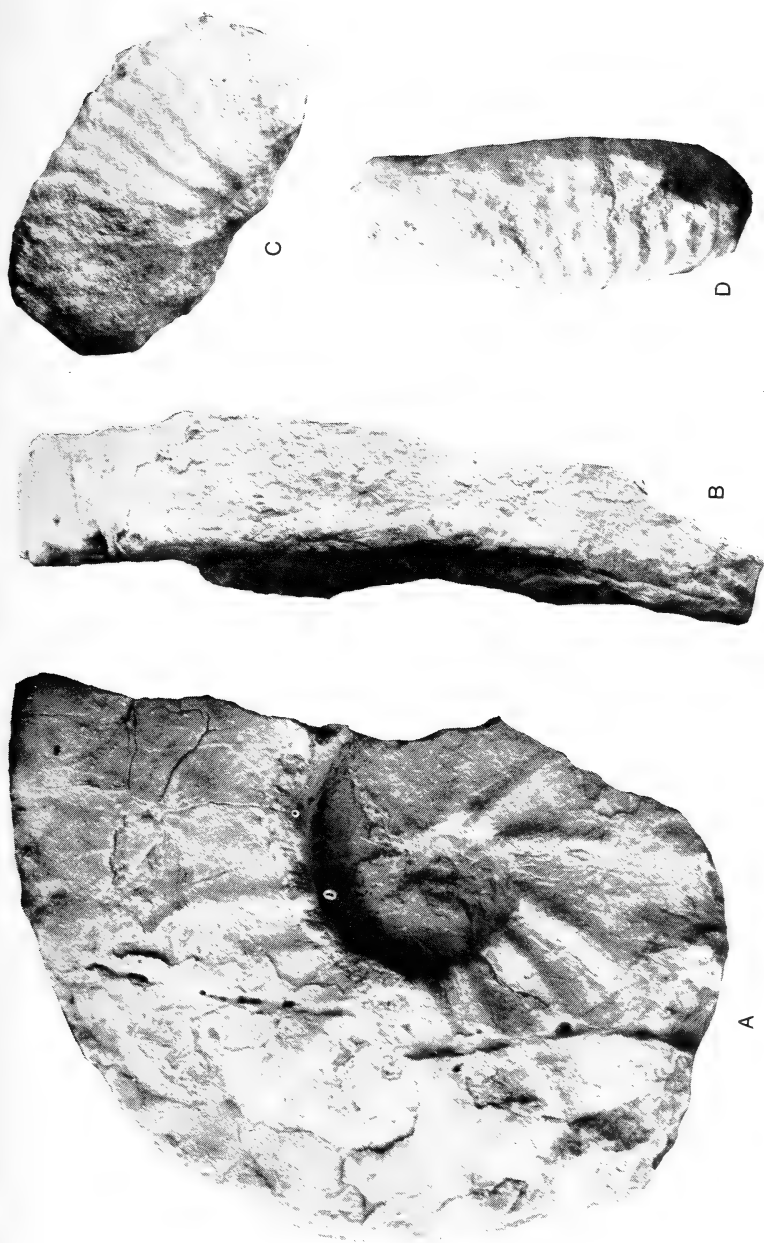


Fig. 9

A-B. ?*Acanthoceras* sp. aff. *tunetana* Pervinquier. Lateral and ventral views of SAM K2558, showing complete absence of ventral tuberculation, tabulate venter, and strongly compressed form. Loc. 34. $\times 2/3$. C-D. *Eucalyptoceras* sp. Lateral and ventral views of SAM K2593. Loc. 29/6. $\times 1$.

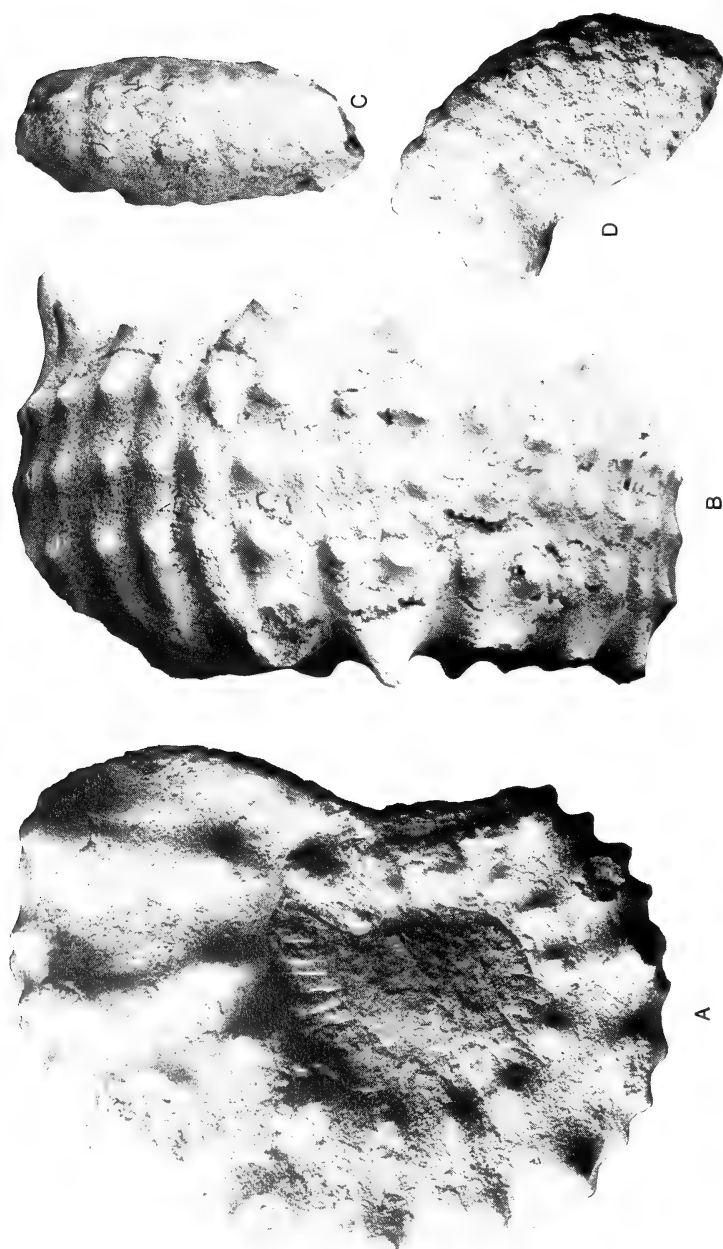


Fig. 10

A-B. *Euomphaloceras cunningtoni meridionale* (Pervinquière). Lateral and ventral views of SAM K2554. Loc. 29/6. $\times 1$.
 C-D. *Eucalycoeras* sp. Ventral and lateral views of SAM K2595. Loc. 29/6. $\times 1$.

are very weak lower ventro-lateral tubercles and upper ventro-lateral clavi. The venter is not preserved.

The second example, SAM K2595, would appear to have similar flank ornament to the above specimen, whilst also showing the nature of the venter. The latter is flattish with distinct upper ventro-lateral clavi joined across the venter by ribs which show faint siphonal swellings.

Measurements

No.			D.	H.	W.	Uo.	Ui.	T.
SAM K2593	?	22	19	?	?	?
SAM K2595	?	23	20	?	?	21

Discussion

The undoubtedly evolute, high-whorled form and flat flanks suggest that the above specimens belong to *Eucalycoceras* rather than *Calycoceras*. The appearance of this genus in the *Turrilites acutus* assemblage is at an earlier stage than any British occurrence. According to Kennedy (1971: 81) '... the earliest English *Eucalycoceras* appear at the top of the *rhotomagense* Zone'. *E. gothicum* (Kossmat) has umbilical tubercles projecting into the umbilicus; *E. pentagonum* (Jukes-Browne) has less flexuous, denser ribbing which is effaced at mid-flank at about the growth stage of the Angolan specimens. It also has more prominent siphonal tuberculation, as well as being an Upper Cenomanian form. *Eucalycoceras rowei* Spath is also an Upper Cenomanian form, closely resembling the above specimens, but also with denser, less flexuous ribbing.

Subfamily *Acanthoceratinae* Hyatt, 1900

Genus ACANTHOCERAS Neumayr, 1875

Type species: *Ammonites rhotomagensis* Brongniart, 1822

Acanthoceras cf. *tunetana* Pervinqui re

Figs 2F-G

cf. *Acanthoceras confusum* (Gu ranger) var. *tunetana* Pervinqui re, 1907: 268, pl. 13, figs 4a, b.
cf. *Acanthoceras tunetana* Pervinqui re, Kennedy, 1971: 90, pl. 40, fig. 5.

Description

Numerous crushed fragments preserved in green shales would appear closest to this species. However, the state of preservation of the Angolan material leaves much to be desired and comparison is difficult.

The largest and best-preserved specimen, SAM K2928, was almost certainly very compressed and evolute. The umbilical wall is steep, with a subrounded umbilical shoulder. The flanks are broad and flat, with a narrow, tabulate venter. Ornament comprises sharp, well-rounded ribs which begin

close to the umbilical seam, and pass backwards (rursiradiate) to the umbilical shoulder where they swell slightly to form distinct umbilical bullae. There are occasional intercalated ribs. From the bullae slightly prorsiradiate, convex forwards, ribs pass up the flanks to prominent, swollen lower ventro-lateral tubercles. Faint ribbing joins the lower ventro-lateral tubercles across the narrow, almost flat venter, and is ornamented with weak upper ventro-lateral clavi. There is no sign of siphonal tuberculation.

Abundant smaller examples, presumably assignable to this species, all very fragmentary and crushed, differ only in having closer, more prominent ribbing and much weaker tuberculation.

A complete, but somewhat crushed example, SAM K2558 (Figs 9A-B) shows similarities to the other Angolan forms and is thus doubtfully included within this genus. This specimen is strongly compressed and very evolute. The umbilicus is rather wide and shallow with a rather broad, vertical umbilical wall and an angular umbilical shoulder. The broad flanks are flat and parallel. The ventro-lateral shoulders are acute, with a narrow, tabulate venter. Ornament on this specimen comprises fairly prominent umbilical bullae which give rise to distinctly prorsiradiate ribs that fade away before mid-flank. There is no other sign of ornament. This specimen differs from the above described material largely in the absence of tuberculation. The acute nature of the ventro-lateral shoulder furthermore seems to suggest that the lack of tuberculation is not due to erosion. Consequently, even the generic assignation of this specimen becomes difficult.

Measurements

No.		D.	H.	W.	Ui.	T.
SAM K2558	..	132	55	± 28	35	?

Discussion

The distant ribbing, compressed form and prominent lower ventro-lateral tubercles of this form are characteristic. *Euomphaloceras alvaradoense* (Moreman) (Stephenson 1955: 63, pl. 7, figs 1-9) from the uppermost Cenomanian basal Eagle Ford of Texas bears a superficial resemblance, presumably due to convergence.

Kennedy (1971) assigned a specimen from the *Turrilites acutus* faunal assemblage of southern England to *Acanthoceras tunetana*, but it differs from the type, and the Angolan material, in having swollen, rounded umbilical tubercles and not bullae.

The Angolan example figured differs from the type in having slightly closer ribbing, being more compressed and having prorsiradiate, not rursiradiate, ribbing.

Genus EUOMPHALOCERAS Spath, 1923

Type species: *Ammonites euomphalus* Sharpe, 1855*Euomphaloceras cunningtoni meridionale* (Stoliczka)

Figs 10A-B; 11; 12A-B; 13A

Ammonites meridionalis Stoliczka, 1864: 76, pl. 41, figs 1a-c.*Acanthoceras meridionale* (Stoliczka) Pervinqui re, 1907: 278, pl. 15, figs 2-6.*Euomphaloceras meridionale* (Stoliczka) Matsumoto *et al.*, 1969: 272, pl. 33, figs 1, 2; pl. 34, fig. 1; text-fig. 6.*Euomphaloceras cunningtoni meridionale* (Stoliczka) Kennedy, 1971: 93.*Description*

This species is the most abundant of the well-preserved acanthocerates from these beds. The shell is very evolute and strongly depressed, with a sub-rectangular intercostal section. The costal section is angular, polygonal. The umbilicus is wide and deep, with a steep umbilical wall and rounded umbilical shoulder. The flanks are flat and parallel, and rather narrow. The venter is broad and slightly convex.

All the specimens are preserved as composite internal moulds. External ornament comprises distinct umbilical bullae, which extend very faintly on to the umbilical wall. On the earlier growth stages these bullae are weakly connected to prominent lower ventro-lateral spines on the ventral shoulder, by single, radial ribs. From the lower ventro-lateral spines, ribs arise in looped pairs, occasionally with an intercalated rib between spines. Each rib is ornamented with upper ventro-lateral and siphonal tubercles. Thus, at about 80 mm diameter, in SAM K2554, there are 19 upper ventro-lateral and siphonal tubercles associated with only 9 lower ventro-lateral spines. At this stage the latter point diagonally outwards.

With age the siphonal tubercles disappear and the ventro-lateral tubercles amalgamate to form prominent horns. At this stage the flank ribs become much more prominent and robust. The suture-line is preserved in SAM K2552 and is reproduced in Figure 11.

Measurements

No.	D.	Hc.	Hi.	Wi.	Wc.	Ui.	Uo.	T.
SAM K2552 ..	±120	54	45	60	71	±60	?	?
SAM K2554 ..	81	33	29	44	48	31	45	?
SAM K2554 ..	±50	20	20	33	38	15	26	?
SAM K2557 ..	?	64	57	67	79	?	?	54

Discussion

Euomphaloceras cunningtoni meridionale (Stoliczka) differs from *E. cunningtoni cunningtoni* (Sharpe) in that the latter has more siphonal than upper ventro-

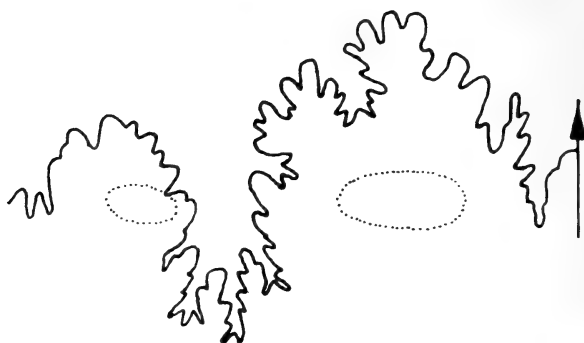


Fig. 11

Suture-line, slightly eroded, of *Euomphaloceras cunningtoni meridionale* (Pervinquière), SAM K2552. $\times 1$.

lateral tubercles. Both these varieties are well treated by Kennedy (1971). The holotype is from the top of the *Turrilites costatus* faunal assemblage of Wiltshire.

Aptychus sp.

Description

A single small *Aptychus* was collected at Novo Redondo in association with indeterminate acanthocerate fragments, *Turrilites costatus* and *Anisoceras plicatile*, and is consequently of low Middle Cenomanian age.

The specimen is preserved as an internal mould, and has a strongly trigonal shape. The inner margin was broken during extraction, but it formed almost a right angle with the harmonic margin. The surface of the mould, i.e. the inner surface of the *Aptychus*, is ornamented with very fine, concentric striae which fade away on the adharmonic ridge.

Discussion

The specimen seems closest to *Spinaptychus* Trauth, but the latter is known only from Senonian beds, commonly in association with *Texanites* (Klinger 1971). Consequently its generic assignation is uncertain.

AGE OF THE FAUNA

The most detailed biostratigraphic subdivision of the Cenomanian is that of Kennedy (1971) for southern England. This author has recognized 5 biostratigraphic zones:

Upper Cenomanian:

Metoicoceras gourdoni Zone

Metoicoceras gestlinianum Zone

Calycoceras naviculare Zone



Fig. 12

A-B. *Euomphaloceras cunningtoni meridionale* (Pervinqui re). Lateral and ventral views of fragment of outer whorl of mature individual, SAM K2557, showing coalescence of ventro-lateral tubercles to form horns, and disappearance of siphonal tubercles. Loc. 29/6. $\times 2/3$.

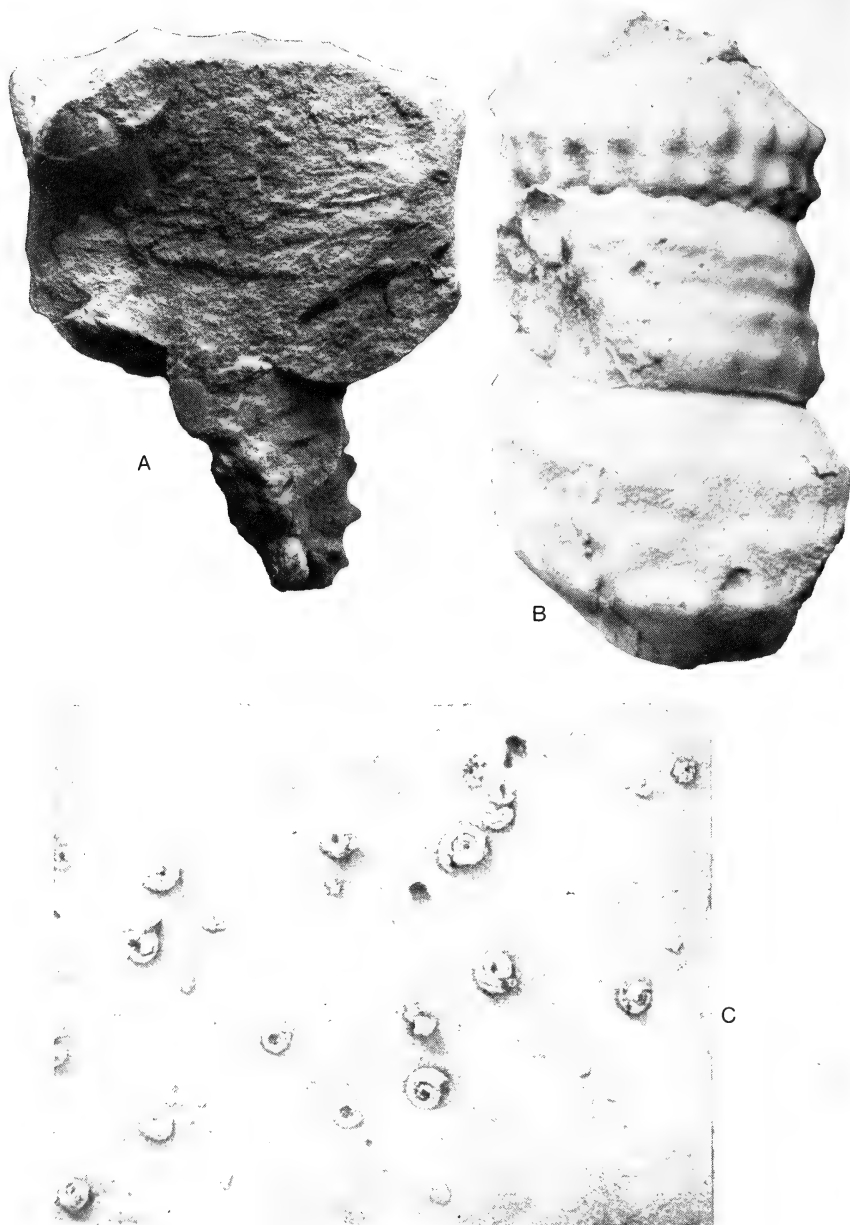


Fig. 13

A. *Euomphaloceras cunningtoni meridionale* (Pervinquière). Front view showing whorl section of SAM K4106. Loc. 29/6. $\times 1$. B. *Turrilites* (*Turrilites*) *acutus* Passy. ?Aberrant specimen SAM K2543 showing shallow spiral groove at about mid-whorl on body chamber. Loc. 29/6. $\times 1$. C. Tiny ammonite nuclei, probably acanthoerate, crowded on bedding plane. SAM K2695. Loc. 29/4. $\times 2$.

Middle Cenomanian:

Acanthoceras rhotomagense Zone

Lower Cenomanian:

Mantelliceras mantelli Zone

Confined to the Lower Cenomanian are the genera *Mantelliceras*, *Sharpeiceras* and *Hyphoplites*, while the heteromorph *Hypoturritites* is particularly abundant in this stage. The strata near Novo Redondo yielding *Mantelliceras* cf. *saxbii* may therefore be assigned to this stage.

The Middle Cenomanian is marked by the appearance of the genera *Acanthoceras* and *Calycoceras*. Kennedy (1971: 102) recognized three stratigraphically separate faunal assemblages within this zone, some of the more important faunal constituents of which are listed below:

Acanthoceras jukesbrownei faunal assemblage:

Acanthoceras jukesbrownei (Spath) and related forms dominate this assemblage, together with *Scaphites equalis* J. Sowerby and *Calycoceras* spp. *Turritites costatus*, *T. acutus* and *T. scheuchzerianus* Bosc are all rare.

Turritites acutus faunal assemblage:

Acanthoceras rhotomagense (Brongniart) and related forms are common in this assemblage which is characterized by the abundance of *T. acutus*. Also common are *Calycoceras paucinodatum* (Crick), *C. newboldi* (Kossmat) and related forms, *Austiniceras austini* (Sharpe), etc., while *Euomphaloceras cunningtoni*, *Forbesiceras obtectum*, *Turritites costatus* and *Acanthoceras tunetana* have been recorded.

There is little doubt that the faunas at Novo Redondo, characterized by the abundance of *Turritites acutus* and *Forbesiceras obtectum*, correspond to this faunal assemblage.

Turritites costatus faunal assemblage:

Especially common in this assemblage are *Turritites costatus*, *Sciponoceras baculoide* (Mantell), *Anisoceras plicatile*, and *Acanthoceras* of the *rhotomagense* group. It seems likely that the crushed fauna occurring in green shales around the chapel at Novo Redondo may be assigned to this faunal assemblage.

Thus, not only are the faunal associations at Novo Redondo virtually identical with those recorded by Kennedy (1971) from southern England, but the same ammonite succession may also be recognized, thereby providing ample evidence for the validity of this biostratigraphic zonation.

The well-documented Cenomanian ammonite faunas of Madagascar (Collignon 1964) are at present of little biostratigraphic value, since the zonal scheme recognized by Collignon (1964) undoubtedly represents collecting from different palaeontological horizons. Most of the Angolan species are, however, known from this island.

From Zululand Crick (1907) has recorded a rich *Turritites acutus* faunal assemblage, dominated by *Calycoceras* spp., *T. acutus*, *Acanthoceras* of the *rhotomagense* group, together with *T. costatus*, *T. scheuchzerianus*, *Forbesiceras largillierianum* (d'Orbigny), etc.

SUMMARY

A typical Cenomanian fauna characterizes Novo Redondo and environs. The lowest beds, although poorly fossiliferous, have yielded examples of the Lower Cenomanian *Mantelliceras* cf. *saxbii* (Sharpe). A higher horizon at Novo Redondo itself contains *Turrilites costatus* Lamarck and *Anisoceras plicatile* (J. Sowerby), and is correlated with the *Turrilites costatus* faunal assemblage of low Middle Cenomanian age. To the north and south of the town alternating limestones and shales are rich in *Turrilites acutus* Passy, *Euomphaloceras cunningtoni* (Sharpe), *Forbesiceras obiectum* (Sharpe), *Calycoceras annulatum* Collignon, *Acanthoceras* cf. *tunetana* Pervinqui re, and *C. coleroonense percostata* Collignon. No higher beds were recorded from this area. The ammonite succession and faunal associations are virtually identical with those recorded from southern England by Kennedy (1971).

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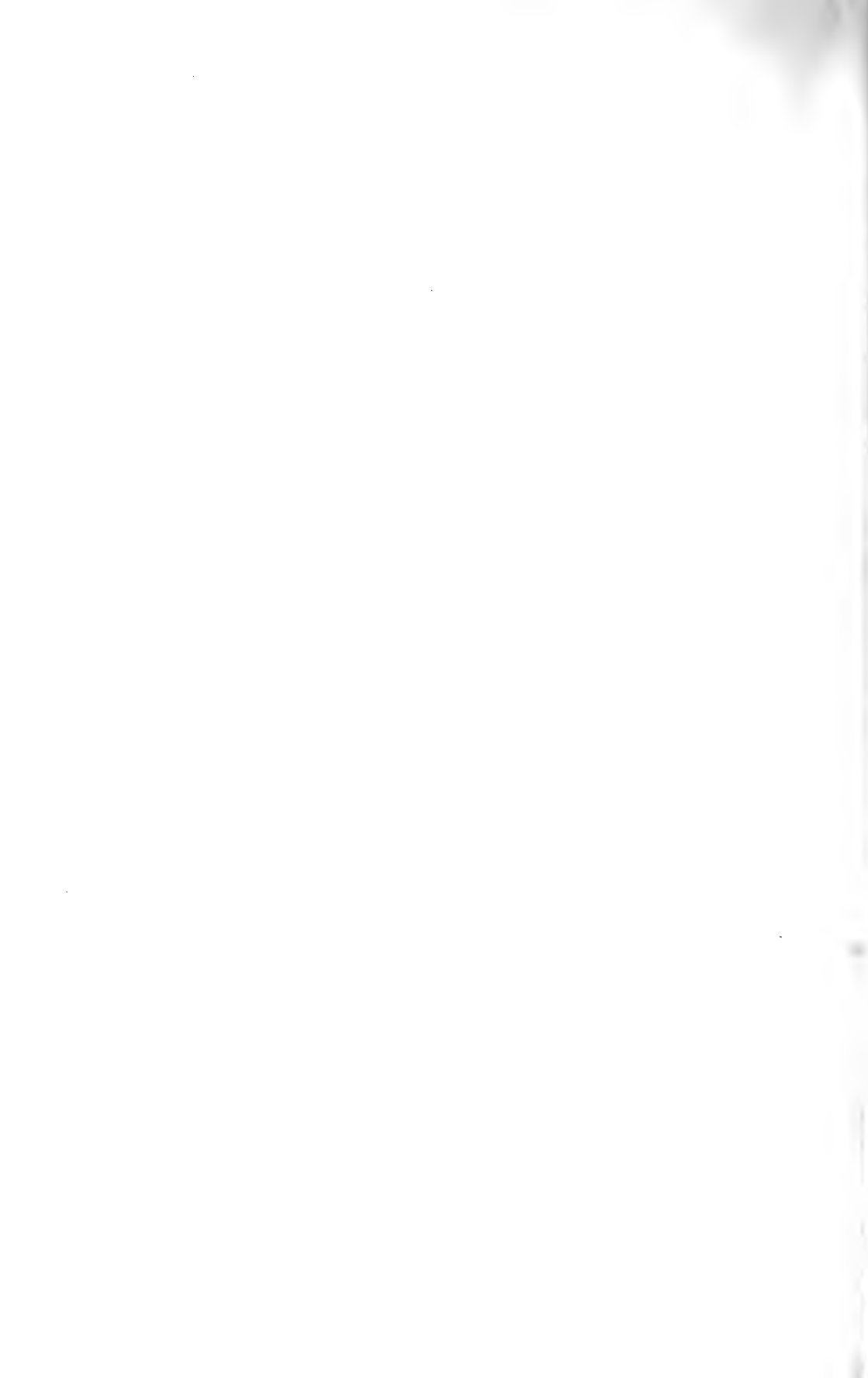
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Michael R. Cooper

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FROM NOVO REDONDO, ANGOLA

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SOUTH AFRICAN PARASITIC COPEPODA

By

BRIAN KENSLEY

South African Museum, Cape Town

&

JOHN R. GRINDLEY

Port Elizabeth Museum, Port Elizabeth

(With 35 figures)

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INTRODUCTION

A comprehensive account of South African parasitic Copepoda was published by the late K. H. Barnard in 1955 (Barnard 1955*a*). In this paper the majority of the species known up to that date were described and figured. Many other papers including Bannister & Grindley (1966), Barnard (1948, 1955*b*, 1957), Calman (1908), Ho (1972), Kensley (1970), Paterson (1958), and Stebbing (1900, 1905) also describe parasitic Copepoda from the South African region.

Since 1955 many more species have been added to the collections of the

South African Museum. The authors and various ichthyologists on the staff of the South African Museum including Dr P. A. Hulley, Mr S. Kannemeyer, Dr M.-L. Penrith, Mr M. Penrith, and Dr F. Talbot collected many of the specimens. Dr D. Eccles collected a large number of specimens from fish caught by anglers, commercial line boats, and trawlers between 1951 and 1953 while he was at the University of Cape Town. Many specimens from game fish and sharks were obtained during the long-line game-fish survey carried out by the South African Museum under the direction of Dr F. H. Talbot in 1960 and 1961. A large collection of specimens of the genus *Pennella* were collected from various species of whales by Dr P. Best. The largest contribution, however, was made by Dr Mary-Lou Hanson Pritchard of the University of Nebraska during six months of collecting in 1961. Dr Pritchard visited South Africa to collect Trematoda parasitic on fishes but agreed also to collect parasitic Copepoda for the second author. Her intensive and meticulous collecting brought many new records and several new species to light.

This study was initiated by the second author but the preparation of this paper has been almost entirely the work of the first author. Preliminary drawings for this work were prepared by Mr M. Leiserowitz but the final drawings are the work of the first author. That a further study of South African parasitic Copepoda was required is clearly evidenced by the description here of no less than fourteen species new to science.

A catalogue of all the species of parasitic Copepoda in the South African Museum is provided, giving details of the material, localities, hosts, catalogue numbers, and type material. Full descriptions and figures are given of species new to science and descriptions are also given of species recorded for the first time from South Africa, and of species that were previously inadequately described.

The nomenclature of the parts of parasitic Copepoda and in particular of their mouthparts has given rise to much confusion in the past. The studies of Bocquet & Stock (1963) and Lewis (1969) have done much to clarify the situation and their recommendations are followed in this work.

Order NOTODELPHYOIDA

Family Notodelphyidae

Gunenotophorus blaizei n. sp.

(Fig. 1a-j)

Description

♀. Head bent ventrally, with lateral margins somewhat ventrally produced. Thorax (2nd to 4th segments) strongly inflated, containing eggs. Abdomen 4-segmented, terminal segment slightly dorsally flexed and spinose, caudal rami dorsally curved, apically blunt. 1st antenna with segmentation obscure, apex curved, distally covered with fine, short bristles. 2nd antenna 3-segmented, 2 basal segments broad, terminal segment tapering, with stout apical hook.

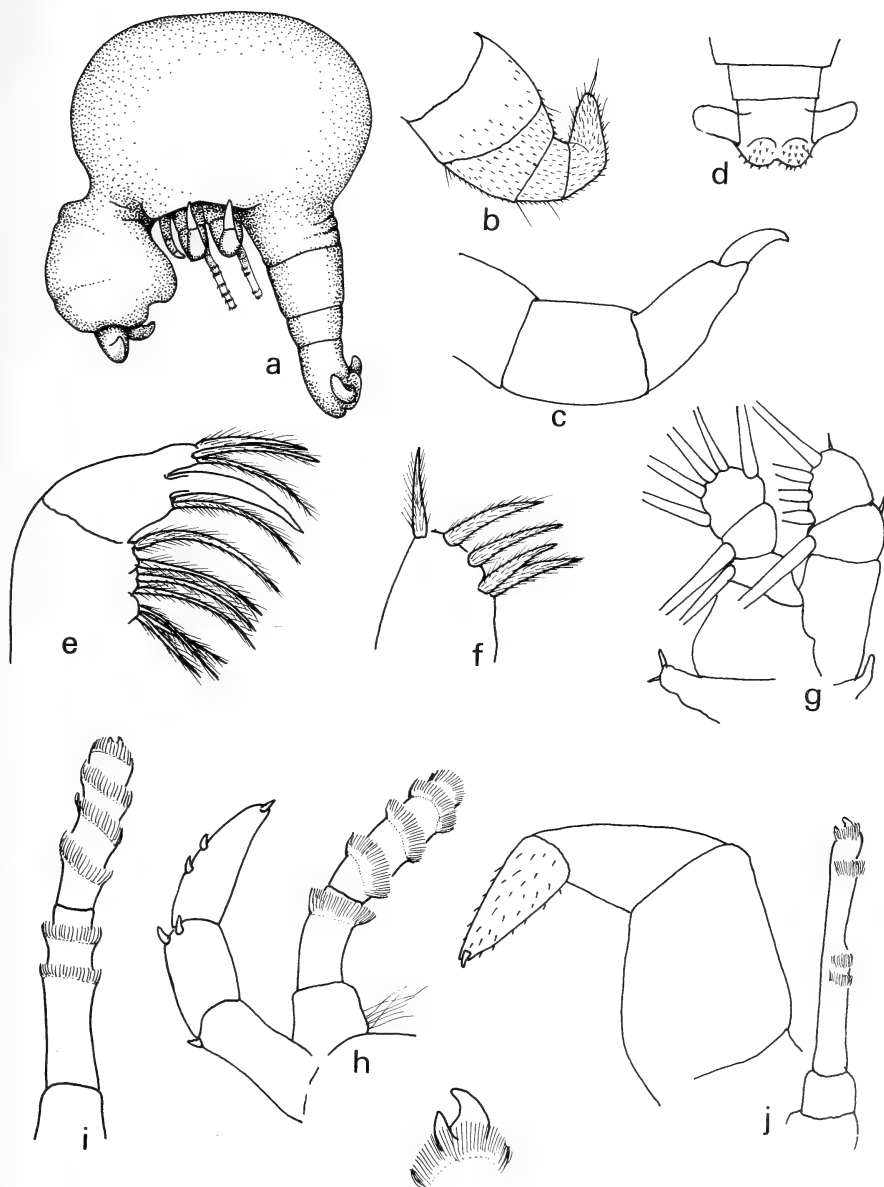


Fig. 1. *Gunenotophorus blaizei* n. sp. a. ovigerous ♀ in lateral view; b. 1st antenna; c. 2nd antenna; d. urosome; e. apex of 2nd maxilla; f. apex of maxilliped; g. 1st thoracic leg; h. 2nd thoracic leg, with apex of endopod further enlarged; i. endopod of 3rd thoracic leg; j. 4th thoracic leg.

Mouthparts agreeing with *G. globularis*. i 1st pair thoracic legs biramous, closely applied to mouthparts, exopod and endopod 3-segmented, both rami bearing long plumed setae. 2nd thoracic legs with endopod slightly longer than exopod, endopod 4-segmented, bearing 5 encircling membranes formed by fused setae on distal half, apex with minute pincer. Exopod 3-segmented, basal segment bearing single distal spine, median segment bearing 2 distal spines, terminal segment armed with 2 spines on outer margin and single apical spine. Exopods of 3rd and 4th legs stout, 3-segmented, flexed dorsally, terminal segment armed with apical spine and numerous minute spinules. Endopod of 3rd thoracic leg 4-segmented, bearing 6 setiferous membranes and apical pincer. Endopod of 4th thoracic leg 2-segmented, basal segment short, distal segment elongate, bearing 4 setiferous membranes and apical pincer.

Material

2 ovigerous ♀♀, from ascidian *Gynandrocarpa unilateralis*, taken in 62 m off Cape St Blaize, N×W½W, 8 km. Total length 1,5–1,8 mm. Holotype S.A.M. A13049, paratype S.A.M. A13041.

Remarks

Although the present species is closely related to *G. globularis* Buchholz, and *G. giganteus* Schellenberg, both of which have been recorded from *Pyura stolonifera* from South Africa, several characteristics demand a specific separation. The size of the largest specimen (1,8 mm) is considerably less than that of *G. globularis* (3–5 mm) or *G. giganteus* (7,2–8,4 mm). The 2nd pair of thoracic legs show some differences. The endopod of *G. globularis* is without spines, or, as in Schellenberg's figure 38 of 1922, with a few minute spinules, while *G. giganteus* is completely unarmed. The condition in the present species, with 1 or 2 spines per segment on the outer margin of the exopod, approaches *G. spinipes* Schellenberg, which also, however, possesses strong spination on the inner margin of the distal segment of the exopod. The markedly-curved terminal segment of the 2nd exopod of *G. curvipes* (Illg 1958) immediately separates it from the present species.

Order CALIGOIDA

Family Caligidae

Caligus cf. *affinis* Heller

(Fig. 2a–g)

Caligus affinis: Brian, 1934: 193, fig. 15; 1939: 178, fig. 1.

Description

♀. Carapace obviously less than half total length. Genital segment flask-shaped, slightly longer than carapace, posterior lobes not very prominent. Abdomen 2-segmented, slightly shorter than genital segment, proximal segment about 3 times length of distal segment. Sternal furca small, arms crescentic.

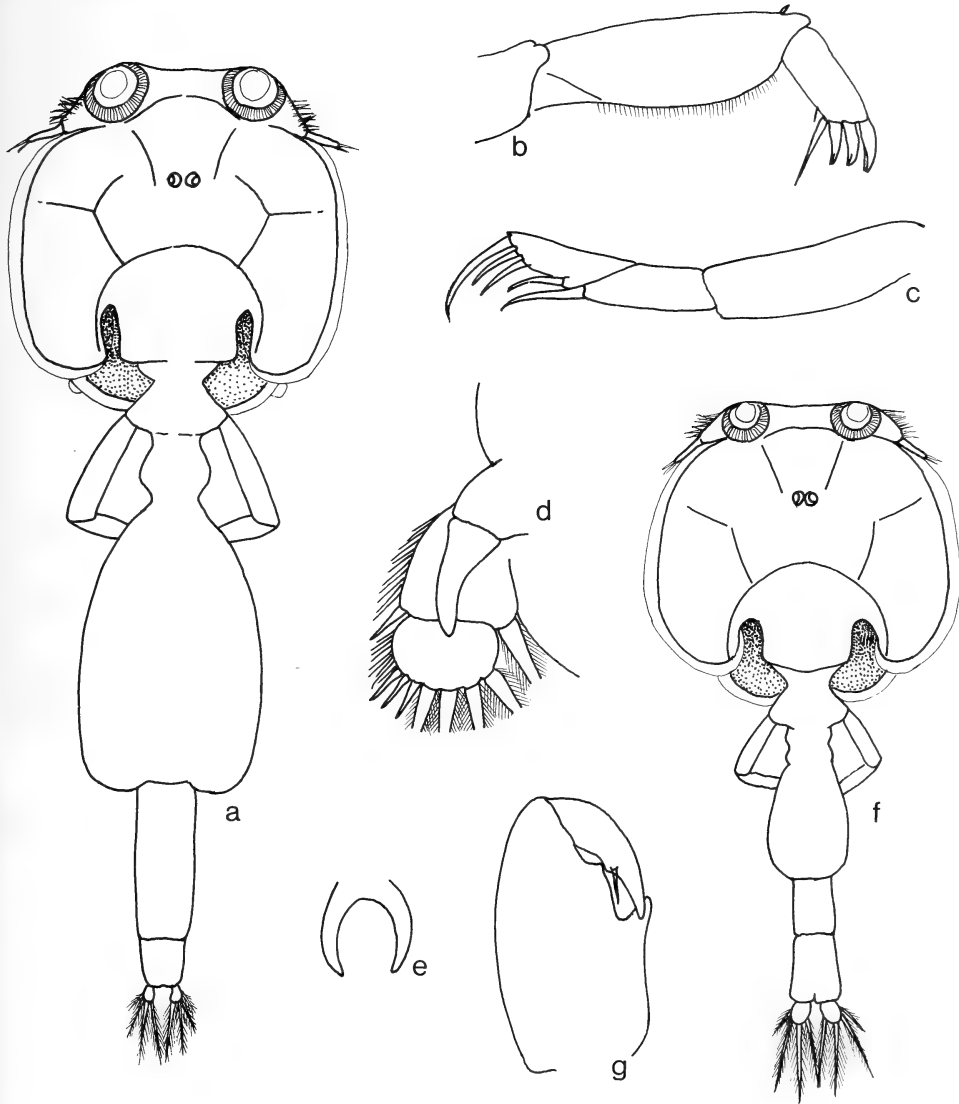


Fig. 2. *Caligus* cf. *affinis* Heller. a. female in dorsal view; b. 1st thoracic leg, ♀; c. 4th thoracic leg ♀; d. 3rd thoracic leg, ♀; e. sternal furca; f. male in dorsal view; g. maxilliped, ♂.

Terminal segment of 1st thoracic leg bearing 3 strong spines, single large simple seta, one minute seta on posterior margin. Penultimate segment with tiny scale-like spine on anterior margin. Spine of exopod of 3rd thoracic leg slightly curved. 4th thoracic leg 3-segmented, terminal segment bearing 4 spines, ultimate spine about twice length of the others, penultimate segment bearing distal spine. Terminal segment of 1st maxilla a simple hooked spine.

♂. Carapace slightly less than half total length. Genital segment flask-shaped but relatively narrower than in ♀. Abdomen 2-segmented, segments equal in length, slightly shorter than genital segment. Maxilliped subchelate, with large blunt thumb-like spine, and second blunt spine on 'palm'.

Material

1 ovigerous + 1♀, 1♂, from *Pomatomus saltator*, Durban. Total length ♀ 4,2-4,4 mm, ♂ 3,0 mm.

Previous records

From *Sphyaena* sp., at mouth of Congo River. From *Umbrina cirrhosa*, from Adriatic and Mediterranean.

Remarks

The present material agrees well with the descriptions of *C. affinis*, and falls within the size range given for ♀♀ (3,30-5,45 mm) by Brian (1934). The only difference appears to be the shape of the genital segment in the ♀, which in the Mediterranean and West African specimens seems to be slightly broader than in the present material.

Caligus aesopus Wilson

(Fig. 3d-f)

Caligus aesopus Wilson, 1940: 72. Hewitt, 1963: 71, figs 4, 5. Yamaguti, 1963: 49, pl. 53, fig. 3.

Material

10 ovigerous ♀♀, 25 ♀♀, 4 ♂♂, from yellowtail, False Bay. Total length ♀ 4,2-5,0 mm, ♂ 3,9 mm.

Previous records

From scombrid (? *Seriola peruana*) from Juan Fernandez. From *Seriola grandis*, New Zealand.

Remarks

The 4-segmented 4th thoracic leg, the shape of the genital segment, with its angular posterior corners, and the single segmented abdomen distinguish this species.

Caligus confusus Pillai

(Fig. 3a-c)

Caligus confusus Pillai, 1961: 104, fig. 10. Kirtisinghe, 1964: 68, figs 70-71.

Caligus alalongae (non Krøyer), Yamaguti, 1954: 379, pl. 2, fig. 19, pl. 3, fig. 21.

Caligus constrictus (non Heller), Wilson, 1937: 25, pl. 3, fig. 3.

Material

1 ovigerous ♀, 2 ♂♂, from gill chamber of *Caranx djedaba*, Durban. Total length ♀ 4,0 mm.

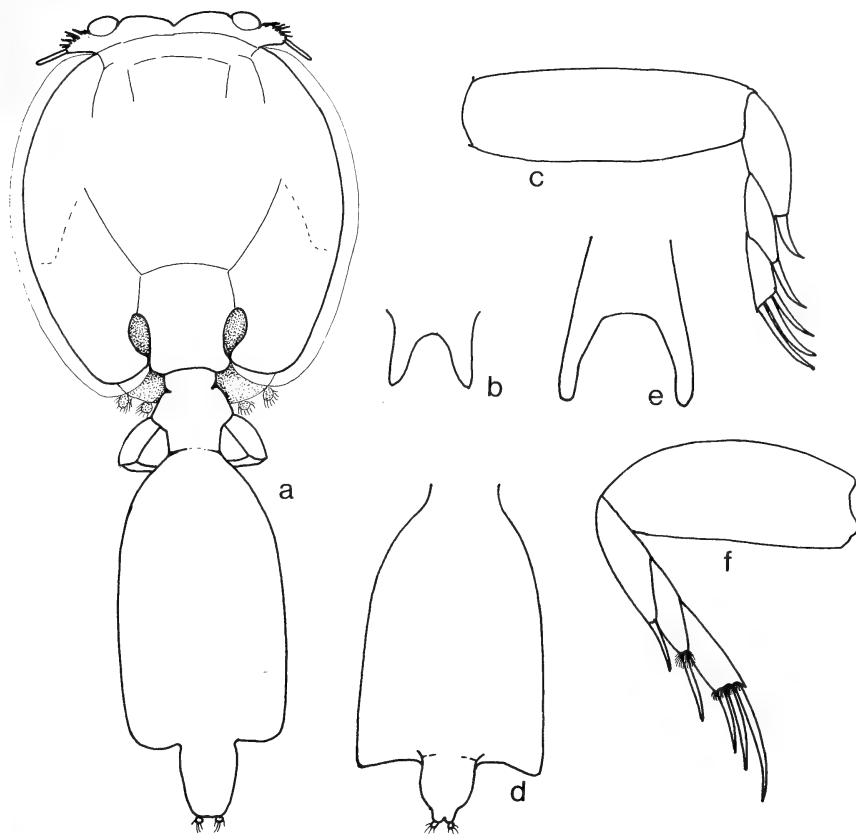


Fig. 3. *Caligus confusus* Pillai. a. female in dorsal view; b. sternal furca; c. 4th thoracic leg, ♀. *Caligus aesopus* Wilson. d. genital segment and abdomen, ♀; e. sternal furca; f. 4th thoracic leg, ♀.

Previous records

From carangids taken from Panang, Galapagos, on *Elagatis* sp. and *Caranx* sp. Celebes, south India.

Caligus coryphaenae Steenstrup & Lütken

(Fig. 4a-f)

Caligus coryphaenae Lewis, 1967: 101, figs 37-39. Pillai, 1962a: 514, fig. 1.

Material

6 ovigerous ♀♀ from *Thynnus obesus*, off Cape Point. 1 ovigerous ♀, 3 ♂♂ from *Euthynnus pelamis*, off Cape Point. Total length ♀ 7.2-8.5 mm, ♂ 5.4 mm. Colour when alive, salmon pink, genital segment and abdomen yellowish.

Previous records

See Lewis (1967: 102)

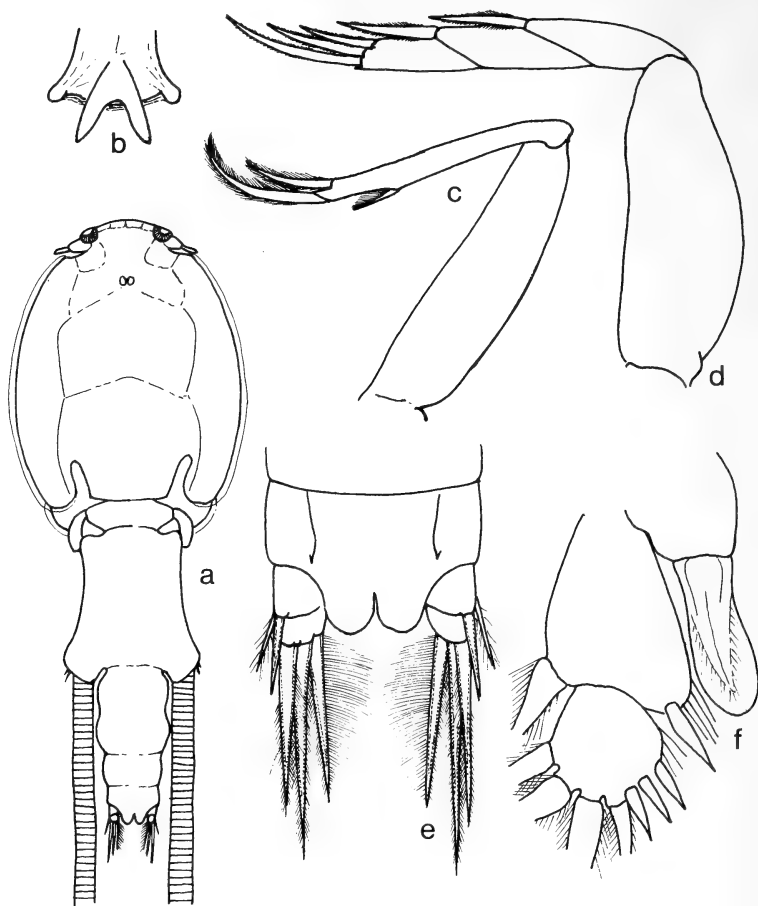


Fig. 4. *Caligus coryphaenae* Steenstrup & Lütken. a. female in dorsal view; b. sternal furca; c. 2nd maxilla, ♀; d. 4th thoracic leg, ♀; e. distal segment of abdomen, ♀; f. 3rd thoracic leg.

Remarks

Three important characters by which this species may be distinguished were given by Pillai (1962a). These are the sternal furca arms which are apically pointed and divergent, the basal hook of the exopod of the 3rd thoracic leg, which is straight or outcurved, and the ultimate claw of the 4th thoracic leg which is obviously longer than the penultimate one. As the present material agrees on all these points, it is placed in this species.

Caligus mortis Kensley

Caligus mortis Kensley, 1970: 167, figs 1, 2.

Material

10 ovigerous ♀♀, taken from intertidal fish from Torra Bay, S.W.A., Möwe Bay, S.W.A., Swakopmund, S.W.A., and Saldanha Bay, Cape. Host species include *Clinus superciliosus*, *Blennius cornutus* and *Chorisochismus dentex*.

Caligus penrithi n. sp.

(Figs 5a, b, 6a-m, 7a-d)

Description

♀. Carapace broadest posteriorly, less than half total length, cephalic region longer than thoracic area. Lunules tiny. Margin with narrow membranous fringe. Posterior sinuses relatively wide. Thoracic region extending well beyond postero-lateral borders. Eyes tiny, contiguous, in anterior half of cephalic area. Free thoracic segment about $\frac{1}{3}$ length of genital segment. Latter slightly broader than long, rectangular, antero-lateral corners more rounded than postero-lateral corners. Abdomen conical, 2-segmented, slightly shorter than genital segment. 1st antenna 2-segmented; basal segment only slightly longer than distal segment, bearing about 12 plumose setae. Terminal segment with 12 distal simple setae. 2nd antenna 3-segmented, basal segment short and broad, middle segment longer and broad, terminal segment tapering, with setule at base of strong falcate process. Mandible indistinctly 3-partite, with 12 subapical denticulations.

Postantennal process a simple spine-like structure. 1st maxilla consisting of broad basal area bearing tiny lobe with 3 setae, and triangular spine-like process. 2nd maxilla 2-segmented, basal segment slightly more than $\frac{1}{2}$ length of distal segment, twice as broad. Distal segment with membranous scale-like process slightly beyond midpoint, 2 distal spines, curved, inner slightly longer than outer, bearing 4 spinules and setiferous fringe, outer spine bearing setiferous fringe only. Maxilliped 2-segmented, basal segment broad, tapering, terminal segment short, bearing strong falciform process, single seta present at distal end of segment. Sternal furca having divergent arms, latter apically truncate, straight-sided. 1st thoracic leg biramous, endopod reduced to tiny process bearing single short spine, on protopodite. Latter consisting of single segment with single proximal plumed seta, shorter than 1st exopod segment. Latter three times longer than wide, with spine at outer distal angle, inner margin bearing fringe of setae. Terminal segment $\frac{1}{2}$ length of 1st segment twice longer than wide, bearing 3 curved distal spines, and 3 stout plumose setae on inner margin. 2nd thoracic leg biramous, both rami 3-segmented. Protopodite 2-segmented, 1st segment less than $\frac{1}{2}$ length of 2nd segment, bearing single plumose seta on inner margin. 2nd segment only slightly longer than wide, with membranous fringe of setae and single stronger seta on inner margin. Basal segment of exopod equal in length to 2 distal segments together, bearing serrate spine at outer distal angle, plumose seta at inner distal angle. Middle segment short, also bearing serrate spine at outer distal angle, plumose seta at inner distal angle. Terminal segment longer than 2nd, bearing 2 simple spines on outer distal margin, 6 plumose setae on distal and inner margin, seta adjacent to spines shortest. Basal segment of endopod bearing single plumose seta on inner margin. 2nd segment longer than basal or terminal segments, with 2 distal plumose setae on inner margin, and pad of closely

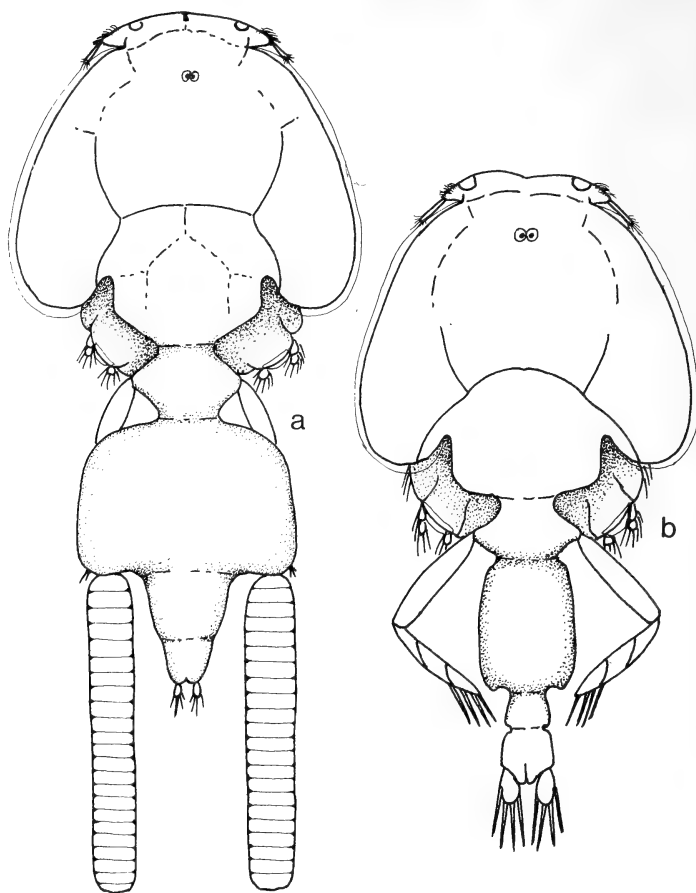


Fig. 5. *Caligus penrithi* n. sp. a. female in dorsal view; b. male in dorsal view.

packed setules around outer margin. Terminal segment with similar smaller pad and 6 plumose setae. 3rd thoracic leg biramous. Protopodite expanded, 2 rami somewhat separated. Exopod 2-segmented, basal segment with distal plumose seta on inner angle and smaller spine at outer distal angle, outer margin fringed with setae. Terminal segment bearing 4 plumose setae and 3 short spines. Hook-like bipartite process arising at base of exopod with fine membranous margin distally. Endopod 3-segmented, basal segment very narrow, with single plumose seta, 2nd and 3rd segments subequal, 2nd segment with 2, 3rd segment with 4 plumose setae. 4th thoracic leg uniramous, 4-segmented, basal segment equal in length to 3 distal segments together, 2nd and 3rd segments each with single fringed spine, terminal segment with 3 slightly curved fringed spines, apex of segment acute. 5th thoracic leg situated at postero-lateral corner of genital segment, consisting of single tiny segment

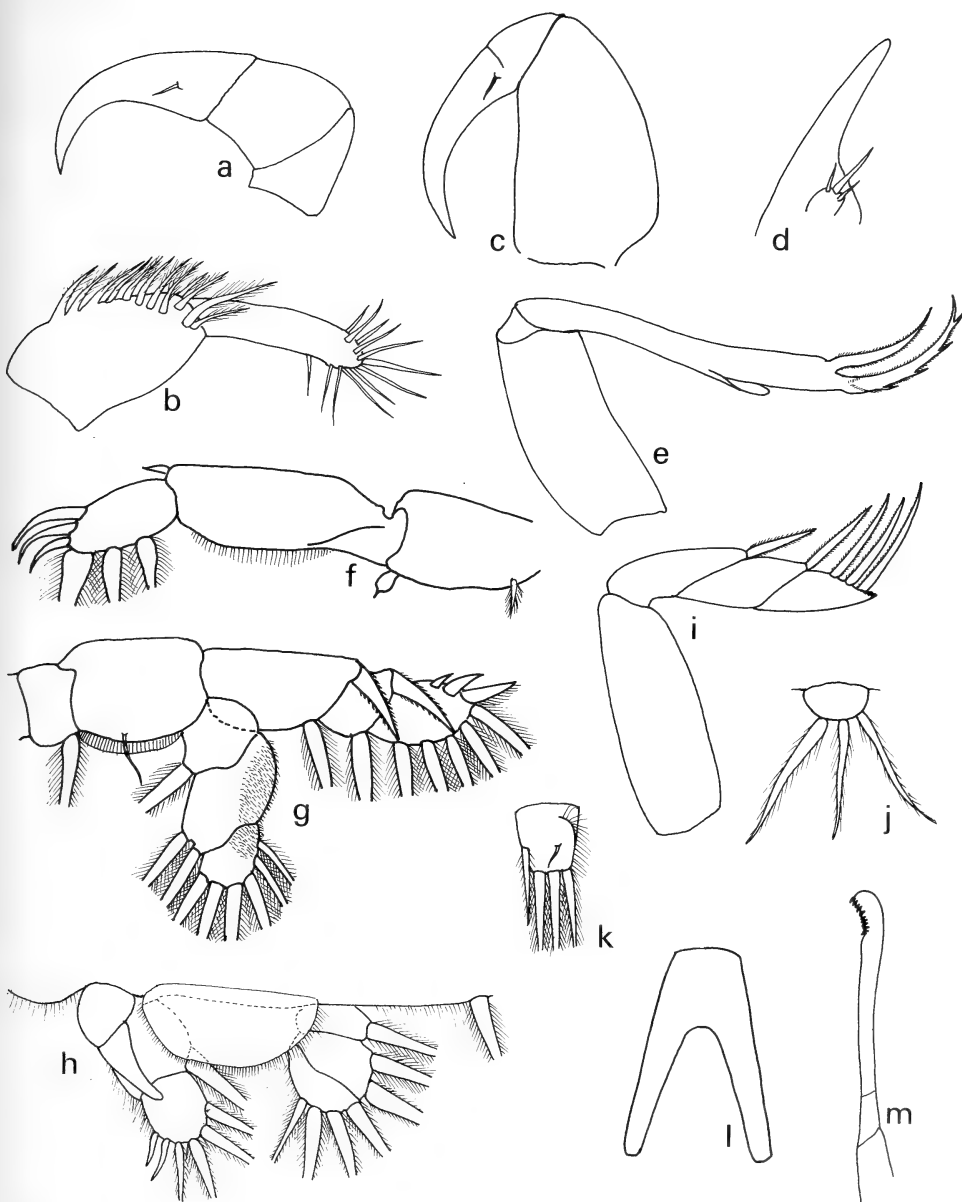


Fig. 6. *Caligus pennithi* n. sp. ♀. *a.* 2nd antenna; *b.* 1st antenna; *c.* maxilliped; *d.* 1st maxilla; *e.* 2nd maxilla; *f.* 1st thoracic leg; *g.* 2nd thoracic leg; *h.* 3rd thoracic leg; *i.* 4th thoracic leg; *j.* 5th thoracic leg; *k.* caudal ramus; *l.* sternal furca; *m.* mandible.

bearing 3 plumose setae. Caudal ramus slightly longer than wide, with 1 simple and 4 plumose setae.

♂. Carapace $\frac{1}{2}$ total length, widest posteriorly, lunules small, margin with narrow membranous fringe, posterior sinuses wide. Thoracic region extending beyond postero-lateral borders. Eyes small, contiguous, in anterior half of cephalic region. Free thoracic segment about $\frac{1}{2}$ length of genital segment. Latter twice longer than wide. Abdomen 2-segmented, segments subequal, narrower than genital segment. 1st antenna 2-segmented, basal segment shorter than terminal segment, bearing about 16 plumose setae on outer margin. Terminal segment with 2 long and 8 short simple setae distally. 2nd antenna 3-segmented, basal segment broad, shorter than middle segment, latter broad, tapering, with 2 distal grooved bulges. Terminal segment short, with short simple seta proximally, plus 2 stout hook-like processes, one elongate the other short. Postantennal process a simple narrowly triangular spine. 1st maxilla a narrow spine-like process, with basal lobule bearing 3 setae. 2nd maxilla as in ♀. Maxilliped 2-segmented, basal segment very broad, with 2 pointed tooth-like processes proximally. Terminal segment short, bearing distal simple seta, and strong slightly curved process which meets tooth-like processes of basal segment. Sternal furca with arms relatively shorter than in ♀, basally slightly curved. 1st thoracic leg biramous, endopod reduced to tiny process bearing 2 terminal spinules. Protopodite consisting of single segment, with small plumose seta proximally, $\frac{2}{3}$ rd length of basal segment of exopod. Latter 2-segmented, with inner margin fringed with setae, and small spine on outer

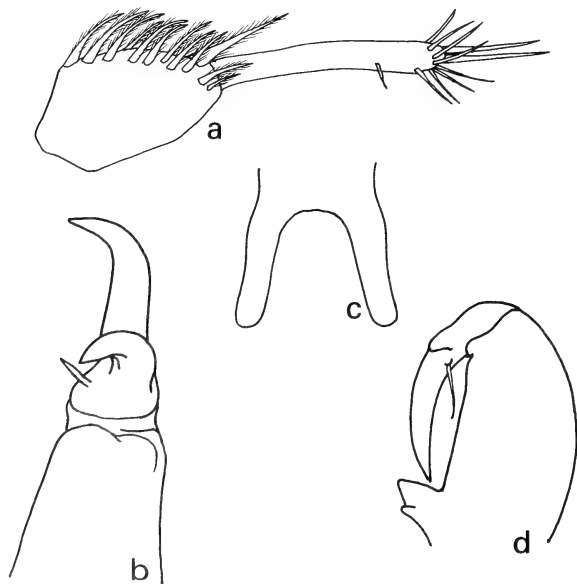


Fig. 7. *Caligus penrithi* n. sp. ♂. a. 1st antenna; b. 2nd antenna; c. sternal furca; d. maxilliped.

distal angle. Terminal segment slightly less than $\frac{1}{2}$ length of basal segment, with 3 curved spines and 3 large plumose setae. 2nd thoracic leg biramous, protopodite 2-segmented, basal segment short, with single plumose seta. 2nd segment with inner margin fringed with setae, and single setae at outer distal angle. Exopod 3-segmented, basal segment equal in length to 2 distal segments together, with strong serrate spine at outer distal angle, and plumose seta at inner distal angle. Middle segment $\frac{1}{2}$ length of terminal segment, carrying single serrate spine, and single plumose seta. Terminal segment with 2 short spines on outer margin, and 6 large plumose setae. Endopod 3-segmented, 1st and 3rd segments subequal, middle segment longer. Basal segment bearing single plumose seta, middle segment with 2 plumose setae and pad of closely packed spinules. Terminal segment with similar pad, plus 6 plumose setae. 3rd thoracic leg biramous, protopodite expanded, bearing setal fringe. Exopod 2-segmented, with bipartite spine-like process at base, basal segment with single plumose seta, terminal segment with 4 plumose setae and 3 small spines. Endopod 2-segmented, basal segment narrow, with single plumose seta, terminal segment with 6 plumose setae and margin of fine hairs. 4th thoracic leg 4-segmented, basal segment slightly longer than 3 distal segments together. 2nd and 3rd segments each with single fringed spine, terminal segment with 3 slightly curved fringed spines, terminal one longest, apex of segment acute. Caudal ramus longer than wide, with 1 small and 4 large plumose setae.

Material

5 ovigerous + 1 ♀♀, 8 ♂♂, from *Chilodactylus fasciatus*, from Möwe Bay, S.W.A. Holotype and allotype S.A.M. A13050, paratypes S.A.M. A13051. Total length ♀ 4.5 mm. Length of egg sacs 2.5 mm. Total length ♂ 3.0 mm.

Remarks

Of the species of *Caligus* having the carapace less than half the total length, and a 2-segmented abdomen about equal in length to the genital segment, the present species most closely resembles *C. robustus* Bassett-Smith. The elongate nature of the genital segment and abdomen of the latter species are very different, however, from *C. penrithi*, with its roughly quadrate genital segment and conical abdomen.

There is some resemblance to *C. djedabae* Rangnekar, particularly in the shape of the carapace and genital segment of the female. The abdomen, however, consists of a single segment, albeit conical, and is relatively shorter than in *C. penrithi*. Other differences also exist in the shape of the sternal furca and the 4th thoracic legs of the ♀.

The species is named for Dr M.-L. and Mr M. J. Penrith of the State Museum, Windhoek, who caught the fish host of this species.

Lepeophtheirus lalandei n. sp.

(Figs 8a, b, 9a-l, 10a-d)

Description

♀. Carapace about $\frac{1}{2}$ total length, obviously longer than wide, sides almost parallel, with moderately wide membranous fringe. Cephalic region longer than thoracic region, with contiguous eyes at about midpoint. Posterior sinuses narrow. Thoracic region extending slightly beyond postero-lateral borders. Free thoracic segment about $\frac{1}{3}$ length of genital segment, wider than long. Genital segment longer than wide, with well-developed posterior lobes, 5th legs just visible beneath these. Abdomen slightly shorter than genital segment, unsegmented, twice longer than wide. 1st antenna 2-segmented, basal segment broadly tapering, bearing about 13 plumose setae on anterior margin, terminal segment shorter than basal segment, with about 12 distal setae. 2nd antenna 3-segmented, basal segment narrow, 2nd segment broad, stout, terminal segment more slender, with simple seta below curved hooked apex, strong spine at base. Postantennal process a small simple slightly curved spine. 1st maxilla bifid, arms short and rounded. 2nd maxilla 2-segmented, basal segment slightly shorter but stouter than terminal segment, latter bearing a rounded scale at midpoint, terminally with 2 curved fringed spines, unequal in length, Mandible slender, with 12 distal denticulations, apically curved. Maxilliped 2-segmented, basal segment stout, terminal segment about $\frac{1}{3}$ length of basal segment, with terminal strongly falcate process, and single seta at base. Sternal furca very small, arms stout, stubby. 1st thoracic leg biramous, endopod reduced to tiny process on protopodite. Latter broad, about same length as 1st exopod segment. Exopod 2-segmented, basal segment twice longer than broad, inner margin fringed with setae, and bearing single short spine at outer distal angle. Terminal segment slightly more than $\frac{1}{2}$ length of basal segment, roughly rectangular, bearing 3 large plumose setae on inner margin, 1 short plumose seta at inner distal angle, and 3 short fringed spines, inner 2 each having an accessory spinule at midpoint. 2nd thoracic leg biramous. Protopodite 2-segmented, basal segment about $\frac{1}{4}$ length of 2nd segment, with single plumose seta on inner margin. 2nd segment with setal fringe on inner margin. Exopod 3-segmented, basal segment equal in length to 2 distal segments together, with 1 plumose seta on inner margin, and strong fringed spine on outer distal angle. 2nd segment similarly armed. Terminal segment with 6 plumose setae and 2 fringed spines. Endopod 3-segmented, middle segment longer than 1st or 3rd. 1st and 2nd segments each with single plumose seta on inner margin, terminal segment with 6 plumose setae. 3rd thoracic legs biramous, protopodite broad and expanded. Exo- and endopod close together. Exopod 2-segmented, basal segment with single plumose seta at outer and inner distal corners. Terminal segment with 3 simple setae, and 4 plumose setae. A broad membranous process at base of exopod, bearing spine on median edge. Endopod 2-segmented, basal segment narrow, with single plumose seta, terminal segment with 5

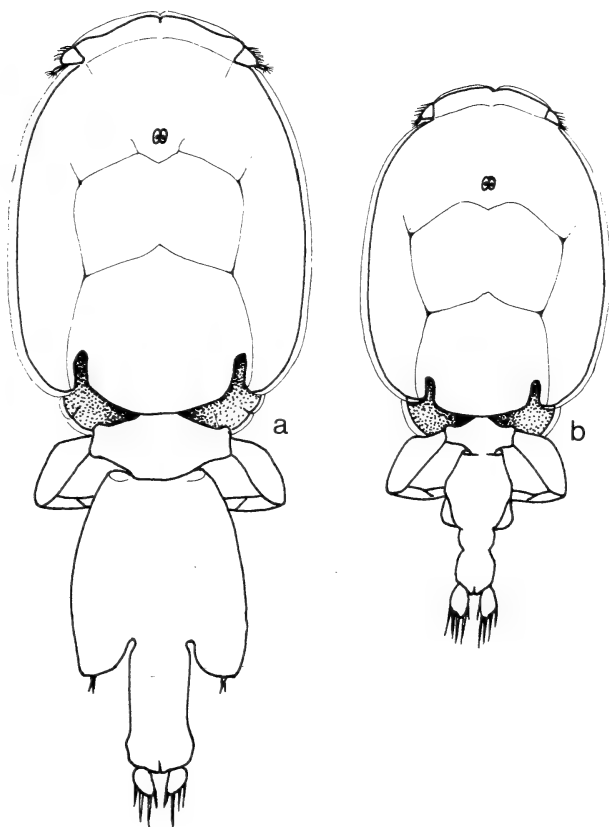


Fig. 8. *Lepeophtheirus lalandei* n. sp. a. female in dorsal view; b. male in dorsal view.

plumose setae. 4th thoracic leg uniramous, 4-segmented, basal segment stout, about twice longer than wide, at least 2–3 times wider than other segments. 2nd segment shorter than 3rd, anterior margin elongated, and joint therefore diagonal, apex of elongation bearing tiny spine and semicircular flange. 3rd segment bearing apically a strong fringed spine with semicircular flange, posterior margin with small spine near apex. Terminal segment bearing 3 strong curved fringed spines, decreasing in size towards anterior margin. Posterior margin bearing 2 small spines at distal end. 3rd and 4th segments both bearing fringe of short fused setae on entire length of anterior margins. 5th thoracic legs situated on ventral surface of genital segment, roughly fig-shaped, bearing apical spine, and 3 plumose setae.

♂. Carapace more than $\frac{1}{2}$ entire length, longer than wide, free thoracic segment wider than long, about $\frac{1}{3}$ length of genital segment. Latter only slightly longer than wide, with flattened flap posteriorly, corresponding to lobes in ♀.

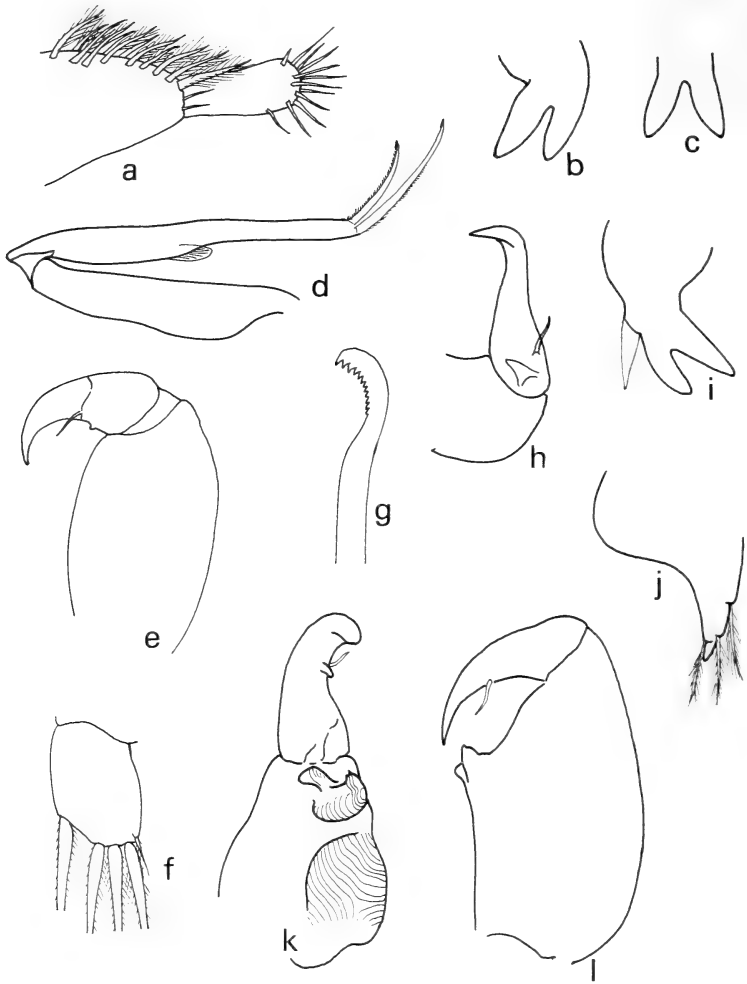


Fig. 9. *Lepeophtheirus lalandei* n. sp. a. 1st antenna, ♀; b. 1st maxilla, ♀; c. sternal furca; d. 2nd maxilla, ♀; e. maxilliped, ♀; f. caudal ramus; g. mandible; h. 2nd antenna, ♀; i. 1st maxilla, ♂; j. 5th thoracic leg, ♀; k. 2nd antenna, ♂; l. maxilliped, ♂.

Abdomen 2-segmented, 1st segment shorter than 2nd. Caudal rami broadly oval, bearing 4 elongate plumose setae. 1st antenna 2-segmented, basal segment slightly longer than terminal segment, with about 12 plumose setae on anterior margin. Terminal segment bearing about 13 simple distal setae. 2nd antenna 2-segmented, apically bearing a curved hook with simple seta, basal segment bearing large proximal ridged area, separated from distal ridged cushion, latter bearing 2 blunt spines, inner one twice length of outer. 1st maxilla bifid, also bearing accessory spine on inner margin. 2nd maxilla as in ♀. Maxilliped subchelate, with short bifid spine on basal segment almost meeting tip of apical

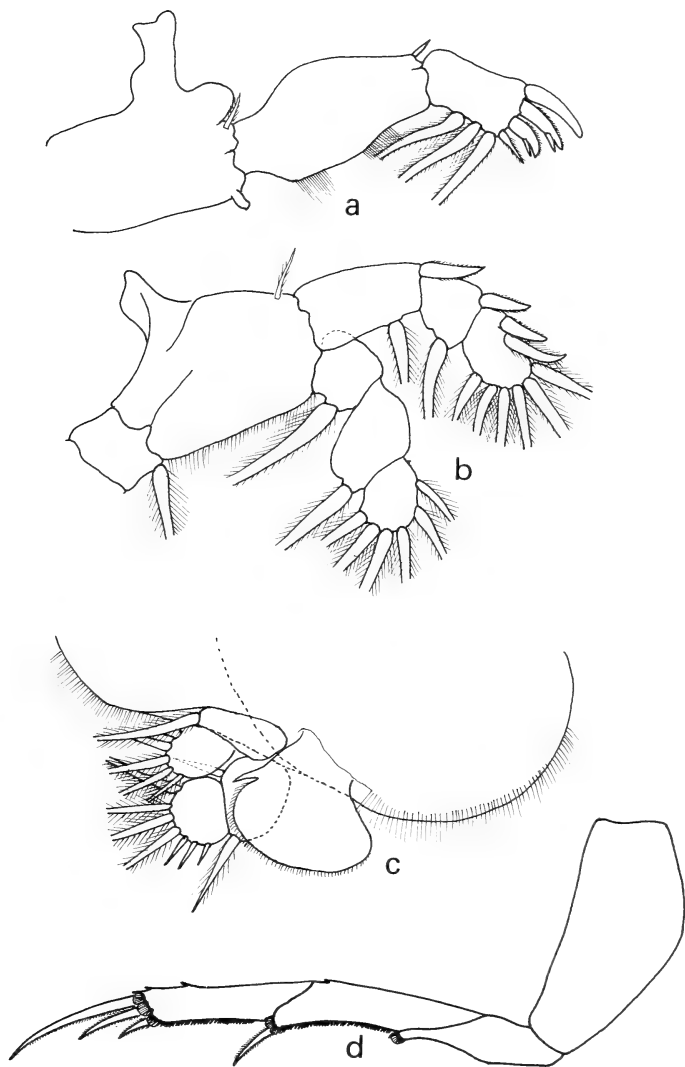


Fig. 10. *Lepeophtheirus lalandei* n. sp. ♀. a. 1st thoracic leg; b. 2nd thoracic leg; c. 3rd thoracic leg; d. 4th thoracic leg.

hook. 1st to 5th thoracic legs as in ♀. Caudal ramus longer than wide, with 1 small and 4 large plumose setae.

Material

7 ♀♀, 1 ♂, from *Seriola lalandi*, taken at Vema Seamount. Holotype and allotype S.A.M. A13052, paratypes S.A.M. A13053. ♀ total length 10,3 mm, carapace length 5,2 mm. ♂ total length 6,4 mm, carapace length 4,0 mm.

Remarks

Of the species of *Lepeophtheirus* in which the carapace is about half the entire length, the present material resembles five species to some degree, viz. *L. argentus*, *L. constrictus*, *L. longipes*, *L. salmonis* and *L. thompsoni*.

L. argentus Hewitt differs from the present species in the carapace shape of the ♀, the 1st maxilla and the segmented abdomen. The male of *L. argentus* has an abdomen much longer than in the present species, does not possess a subchelate maxilliped, has a differently shaped 2nd antenna, and does not possess an accessory spine on the 1st maxilla.

L. constrictus Wilson closely resembles the present species in the shape of the sternal furca, the 4th and 5th thoracic legs, the 1st maxillae, and the undivided abdomen in the female. The carapace shape, however, differs, while the genital segment does not possess posterior lobes. *L. constrictus* at 6.6 mm total length is considerably smaller than the present species.

L. longipes Wilson differs in possessing a segmented abdomen, which is relatively smaller, and in the shape of the sternal furca and 1st maxilla.

L. salmonis Wilson differs from the present species in the relatively shorter segments of the 4th thoracic leg in the female, the undivided 1st maxilla and in the shape of the carapace. The male of *L. salmonis* is very similar to the present species.

L. thompsoni Baird differs in possessing a segmented abdomen, a relatively smaller 4th pair of thoracic legs, in the shape of the furca and 1st maxilla, and in the shape of the carapace in the female.

Lepeophtheirus longispinosus Wilson

(Fig. 11a, b)

Lepeophtheirus longispinosus Wilson, 1908: 604, pl. 52. Yamaguti, 1963: 74, pl. 99, fig. 5.
(non *Lepeophtheirus* sp. of Barnard, 1955a: 252)

Material

3 ovigerous ♀♀ from *Carcharinus leucas*. Total length 2.9–3.0 mm.

Previous records

On *Sphyrna zygaena* from N. America.

Remarks

The character of the 1st maxilla and the furca makes this species easily recognizable. The former is slender, elongate, armed with a slender spine at the base. The furcal arms are widely divergent, apically spatulate, and bear a slender secondary branch on the inner margin.

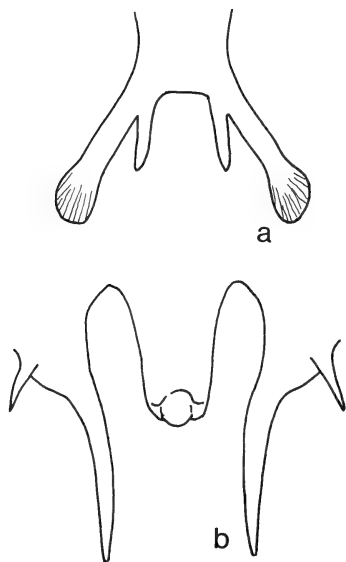


Fig. 11. *Lepeophtheirus longispinosus* Wilson.
a. sternal furca; b. oral cone and 1st maxilla.

***Lepeophtheirus natalensis* n. sp.**

(Figs 12, 13a-k)

Description

♀. Carapace more than half total length, slightly longer than wide, cephalic region longer than thoracic area, with narrow membranous fringe. Eyes situated at posterior end of cephalic region. Posterior sinuses moderately wide. Free thoracic segment about $\frac{1}{3}$ length of genital segment. Latter roughly rectangular, with rounded posterior lobes. Abdomen unsegmented, $\frac{1}{3}$ length of genital segment, longer than broad, with narrow posterior slit. 1st antenna with basal segment slightly longer than terminal segment, former bearing about 19 plumose setae, latter with 12 simple setae distally. 2nd antenna 3-segmented, middle segment bearing striated rounded process, terminal segment bearing simple seta, and tapering hook-like process. Postantennal process a simple stout hook. 1st maxilla flanking oral cone, consisting of simple stout posteriorly-directed hook. 2nd maxilla 3-segmented, 2 distal segments slender, 2nd bearing 2 fringed spines, terminal segment bearing single elongate fringed spine. Maxilliped 2-segmented, basal segment stout, 5 times longer than terminal segment, bearing strongly-curved apical process. Branches of sternal furca slender, divergent, apically rounded. 1st thoracic leg biramous, endopod reduced to tiny process on protopodite. Latter shorter than 1st segment of exopod, with

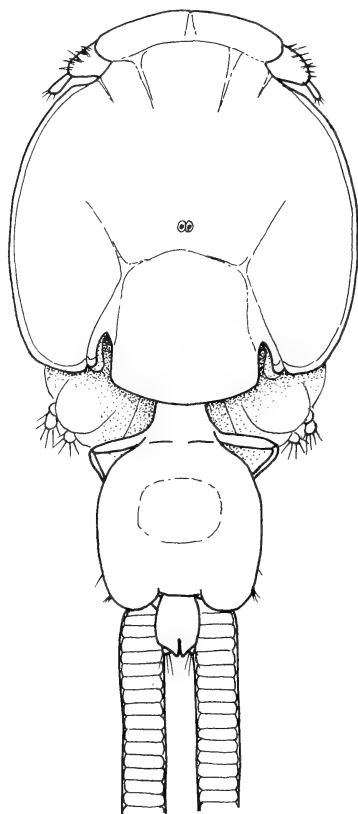


Fig. 12. *Lepeophtheirus natalensis* n. sp.
Female in dorsal view.

short plumose seta at outer distal angle, and at midpoint of posterior margin. Endopod 2-segmented, basal segment bearing fringe of setae on posterior margin, and tiny spine at outer distal angle. Terminal segment bearing 3 large plumose setae on posterior margin, and 1 small simple spine and 3 serrate spines distally, inner 2 each with accessory spinule. 2nd thoracic leg biramous. Protopodite 2-segmented, basal segment $\frac{1}{3}$ length of 2nd segment, with single plumose seta. 2nd segment with setal fringe on posterior margin, and simple spine at outer distal angle. Exopod 3-segmented, basal segment slightly longer than 2 distal segments together, bearing strong fringed spine at outer distal angle, single plumose seta at inner distal angle. 2nd segment similarly armed. Terminal segment with 6 large plumose setae, and 2 short spines. 3rd thoracic leg biramous, protopodite expanded, exopod 2-segmented, basal segment small, bearing single plumose seta, terminal segment with 6 plumose setae and single short spine. Strong bipartite hooked and striated process at base of exopod. Endopod 2-segmented, basal segment narrow, with single plumose seta,

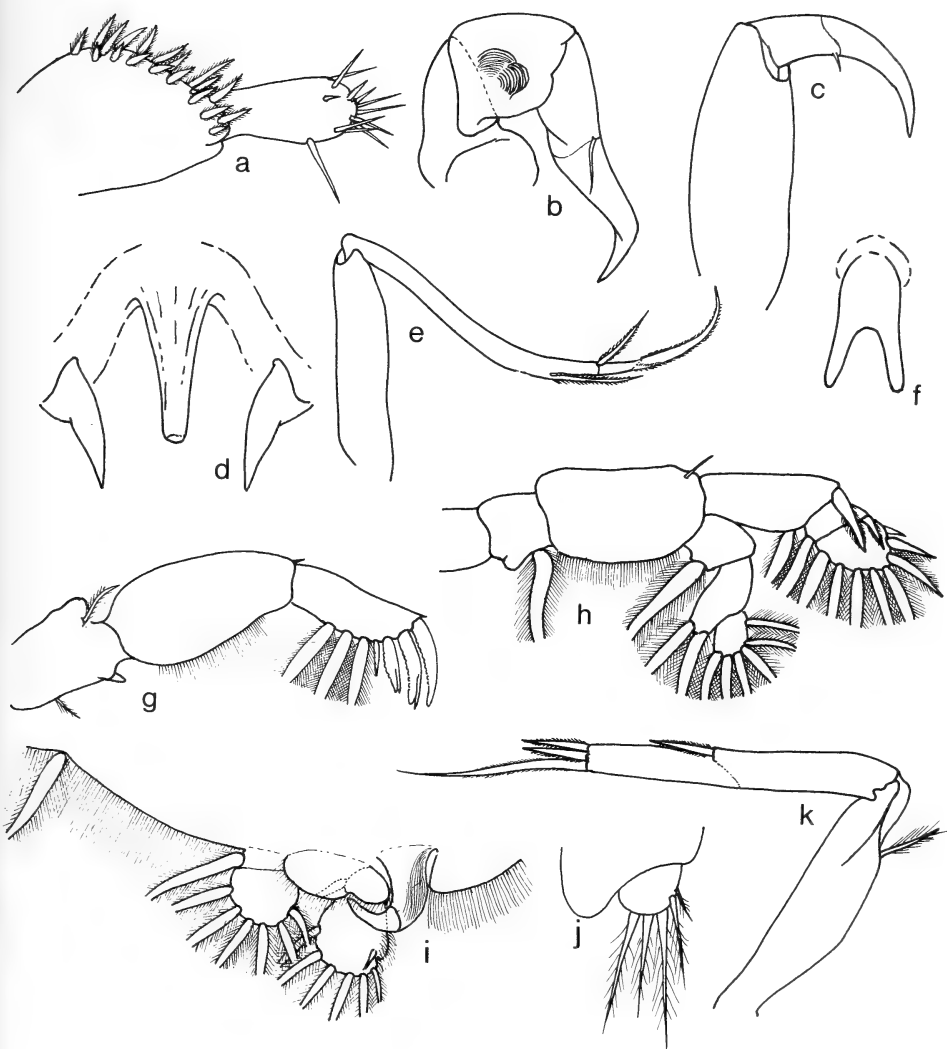


Fig. 13. *Lepeophtheirus natalensis* n. sp. ♀. a. 1st antenna; b. 2nd antenna; c. maxilliped; d. oral cone and 1st maxillae; e. 2nd maxilla; f. sternal furca; g. 1st thoracic leg; h. 2nd thoracic leg; i. 3rd thoracic leg; j. caudal ramus; k. 4th thoracic leg.

terminal segment with 6 plumose setae. 4th thoracic leg uniramous, 3-segmented, basal segment slightly shorter than 2 distal segments together, with single distal plumose seta. Middle segment bearing distal fringed spine. Terminal segment bearing distally 1 long and 2 short fringed spines. 5th thoracic legs reduced to 3 setae on each side of genital segment. Caudal rami very short, rounded, bearing plumose setae.

Material

6 ovigerous ♀♀ from *Carcharinus leucas*, from Natal. Holotype S.A.M. A13054, paratypes S.A.M. A13055. Total length (excluding egg sacs) 5,1–5,2 mm.

Remarks

In general shape and proportions the present species most closely resembles *L. insignis* Wilson, of the species of the genus known from South Africa. It can, however, immediately be distinguished from this and all the other South African species by the 1st maxilla, which is a simple stout spine, and not bifurcate. Amongst the other species of the genus which possess an undivided 1st maxilla and an abdomen of a single segment, this species most closely resembles *L. parviventris* Wilson, from the North Pacific. It differs from this species in the greater length of the furcal arms, and in the 1st maxillae which in the former are bifurcate.

Family **Cecropidae***Cecrops exiguus* Wilson

(Fig. 14a, b)

Cecrops exiguus Wilson, 1923: 1, figs 1–15. Yamaguti, 1963: 89. Shiino, 1965: 381, figs 1–4.

Material

7 ovigerous ♀♀ with attached ♂♂, 9 ♀♀, 3 ♂♂, from *Mola lanceolata*, Bantry Bay, Cape. Total length ♀ 10,0–13,5 mm, ♂ 6,0 mm.

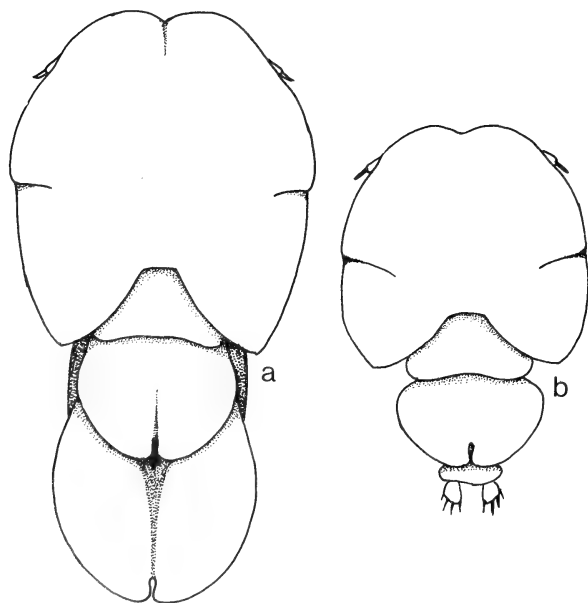


Fig. 14. *Cecrops exiguus* Wilson.
a. female in dorsal view;
b. male in dorsal view.

Previous records

From shark taken off Florida. From *Mola mola*, Japan.

Remarks

Cecrops exiguus may be easily separated from the more common *C. latreillei* being about half the size of the latter species. Differences also exist in the shape of the dorsal plates of both the male and female. The females of *C. exiguus* are pale-ochrous yellow with olive-green ovisacs, while the males are a pale creamy colour.

Family **Euryphoridae***Elytrophora hemiptera* Wilson

(Fig. 15a-d)

Elytrophora hemiptera Wilson, 1921: 4, pl. 2, figs 13-19. Yamaguti, 1963: 103, pl. 123, fig. 2.

Material

1 ♀ from yellowfin tunny, *Thunnus albacares*, Table Bay. 13 ♂♂ from bluefin tunny, *Thunnus thynnus*, 48 km west of Cape Point. Total length ♀ 7.8 mm, ♂ 6.1 mm.

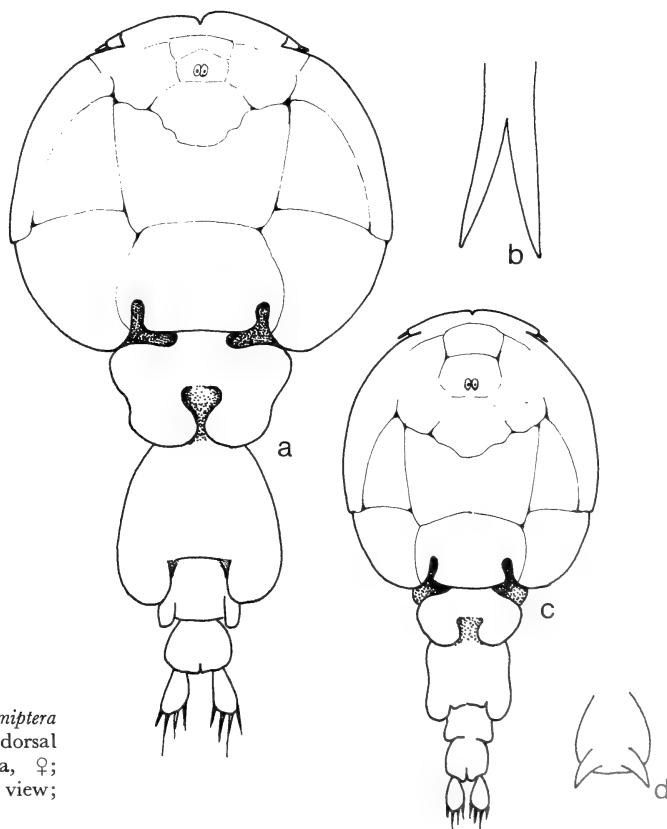


Fig. 15. *Elytrophora hemiptera* Wilson. a. female in dorsal view; b. sternal furca, ♀; c. male in dorsal view; d. sternal furca, ♂.

Previous records

From *Thunnus thynnus*, *Thunnus albacares*, *Isurus glaucus*, Japan.

Remarks

The status of the male specimens is not absolutely certain. They are to some extent intermediate in form between *E. hemiptera* Wilson from Japan and *E. atlantica* Wilson from the North Atlantic. The status of this parasite may be of interest in relation to the status and movements of their hosts in this area. Their colour when alive is light yellowish with fine reticular brown markings giving a general appearance of light brown.

Gloiopotes watsoni Kirtisinghe

Gloiopotes watsoni Kirtisinghe, 1934: 167. Cressey, 1967a: 7, figs 38–39.

Gloiopotes auriculatus Barnard, 1957: 11, fig. 8.

Description

♀. Carapace longer than broad, half total length. Postero-median lobe of thorax with 2 anterior and 1 or 2 posterior spines on each postero-lateral rounded corner. Dorsal plates of 4th thoracic segment completely separate, ear-shaped. Genital segment with row of 3 spines on either side of dorsal convexity. Posterior lobes spinulose on inner surface, usually in single row proximally. Ovate projection on posterior lobes spinose on inner and outer margins. Abdomen 2-segmented, distal segment about twice length of proximal. Latter with 4 dorsal spines, distal segment with 10 dorsal spines, 8–10 lateral spines. Caudal rami elongate, bearing about 11 spines.

♂. Carapace longer than broad, slightly less than half total length. Posterior median lobe of thorax with 2 lateral and 2 posterior spines on each side. Dorsal plates of 4th thoracic segment completely separate, subtriangular, with 3–5 spines near posterior margin. Genital segment as broad as long, with single spine on each side near centre, single smaller spine laterally, 3–4 spines on each rounded postero-lateral corner. Genital segment projections slender, elongate, with about 4 spines on inner (dorsal) margin, 7 on outer (ventral) margin. 3 strong apical spines. Abdomen 2-segmented, proximal segment half length of distal. Former bearing 2 spines, latter with variable arrangement, usually 4 or 5. Caudal rami as in ♀.

When fresh the general colour of the thorax and abdomen is blue with purple markings on the dorsal surface. The egg sacs are salmon pink. They occur most abundantly between the anal fins and around the anus of their host where they may produce extensive wounds.

Material

Numerous ♀♀ and ♂♂, from black and striped marlin (*Makaira indica* and *Makaira audax*), from Cape.

Family **Pandaridae***Echthrogaleus torpedinis* Wilson

(Fig. 16)

Echthrogaleus torpedinis Wilson, 1907: 371, pl. 21. Yamaguti, 1963: 120, pl. 137, fig. 2. Cressey, 1967b: 58, figs 291-294.

Material

3 ovigerous ♀♀, from *Torpedo* sp., taken west of Slangkop, Cape. Total length ♀ 11.4-13.2 mm.

Previous records

From *Tetranarce occidentalis*, east coast of U.S.A.

Remarks

No differences can be found between the present material and the description given by Cressey (1967).

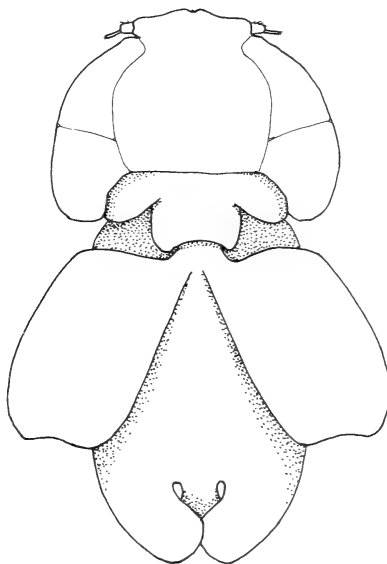


Fig. 16. *Echthrogaleus torpedinis* Wilson.
Female in dorsal view.

Family **Anthosomatidae***Lernanthropodes natalensis* n. sp.

(Fig. 17a-h)

Description

Cephalothorax slightly ventrally flexed, widest posteriorly, rectangular in lateral view. Trunk narrow, cylindrical, about same width as cephalothorax. 1st antenna 7-segmented, bearing several setae. 2nd antenna with uncinate strongly chitinated apical segment, basal segment broadly tapering. Mouth tube

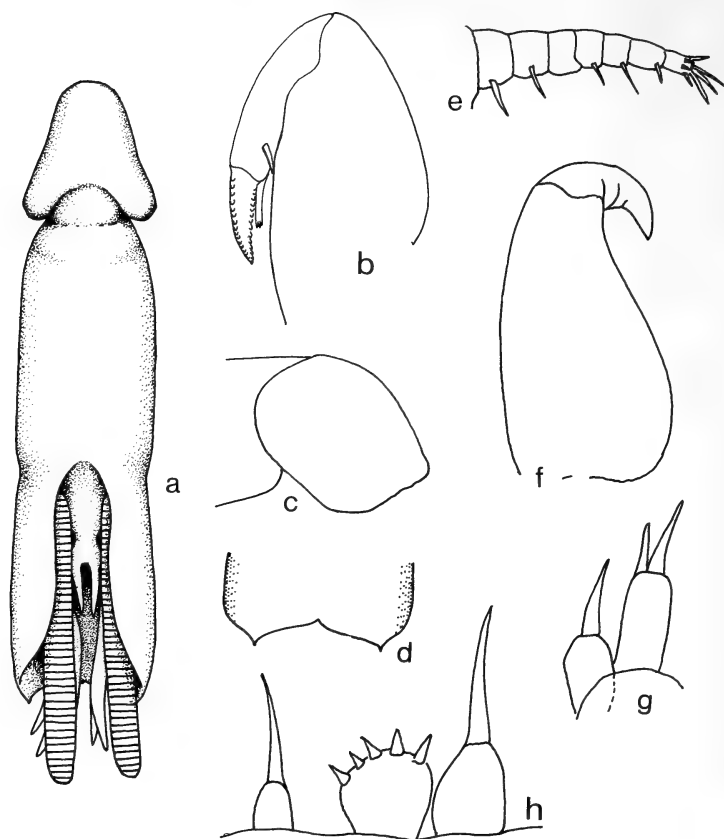


Fig. 17. *Lernanthropodes natalensis* n. sp. a. female in dorsal view; b. 2nd maxilla; c. cephalothorax in lateral view; d. posterior margin of 3rd thoracic leg 'sheath'; e. 1st antenna; f. 2nd antenna; g. 1st maxilla; h. 2nd thoracic leg.

conical. 1st maxilla biramous, each ramus of single segment tipped with setae. 2nd maxilla 3-segmented, terminal segment armed with 2 rows of short spines, median segment with distal seta, basal seta broad. Maxilliped 2-segmented, terminal segment hook-shaped. 1st and 2nd thoracic legs biramous, rami each of one segment, outer segment broader than inner, armed with 5 short spines, inner ramus tipped with single seta, papilla external to exopod bearing single seta. 3rd thoracic legs almost as long as trunk, fused to form broad lamella completely ensheathing genital segment and abdomen ventrally, leaving narrow gap dorsally. Lamella with single point posteriorly on each side. 4th legs inside sheath formed by 3rd legs, biramous, rami fused only at base, lamellar, protruding beyond sheath. Genital segment spindle-shaped. Abdomen slightly shorter than genital segment, with pair of lamellar caudal rami.

Material

1 ovigerous ♀, from *Chorinemus tol*, Durban. Holotype S.A.M. A13034. Total length 3,5 mm. Egg sac length 1,7 mm.

Remarks

Three species of the genus *Lernanthropodes* have been described, viz. *L. cucullus* (Bere 1936) and *L. chorinemi* and *L. trachinoti* (Pillai 1962a). *L. cucullus* has the sheath formed by the 3rd thoracic legs completely enclosing the genital segment and abdomen, and 4th thoracic legs, none of which are ventrally visible. The posterior margin of this sheath is divided into 2 lobes on either side, unlike the present species, which has only a slight median indication of subdivision.

L. trachinoti, taken from *Trachinotus blochii* from India, also has the posterior margin of the sheath divided into 2 lobes on either side, while the cephalothorax is rectangular, rather than triangular as in the present material.

L. chorinemi, recorded from *Chorinemus lysan* from India, closely resembles the present species, but several differences make a specific separation seem desirable. *L. chorinemi*, with a total length of 8,2 mm, is considerably larger than the ovigerous female of *L. natalensis* (3,5 mm). The evenly rounded posterior margin of the sheath in Pillai's species differs from the slightly bilobed condition in *L. natalensis*. Several differences exist in the structure of the appendages. The 1st antenna of *L. chorinemi* has 4 segments, as against the 7 of *L. natalensis*, while the 2nd antenna of the Indian species possesses 3 small spines at the base of the terminal segment, not found in the present species.

Lernanthropus corniger Yamaguti

(Fig. 18a, b)

Lernanthropus corniger Yamaguti, 1954: 387, pl. 4, figs 35-39, pl. 5, figs 40-41; 1963: 148, pl. 161, fig. 1. Pillai, 1963: 660, fig. 3.

Material

11 ovigerous + 10 ♀♀, total length (from 'horns' to end of dorsal plate) 3,4-3,7 mm. From *Caranx djedaba*, Durban.

Previous records

On *Megalaspis* sp., from Macassar, and on *Megalaspis cordyla* from Trivandrum, India.

Remarks

No differences can be detected between the present material and Yamaguti's descriptions and figures. The ventro-lateral extensions of the head forming the prominent 'horns', and the 3 ventral lamellae of the 3rd legs, make this species unmistakable.

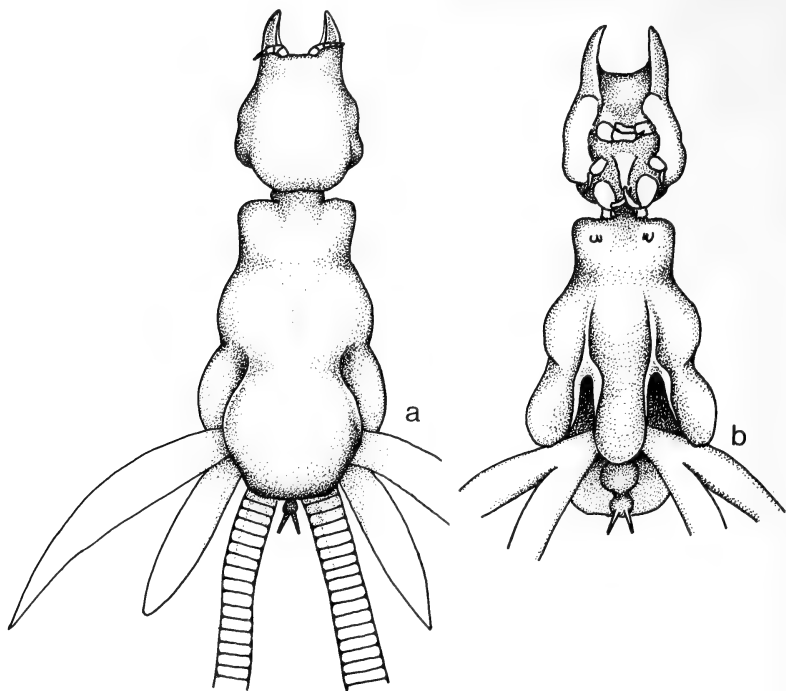


Fig. 18. *Lernanthropus corniger* Yamaguti. *a.* female in dorsal view; *b.* female in ventral view.

***Lernanthropus ecclesi* n. sp.**

(Figs 19a-c, 20a-l)

Description

♀. Body somewhat cylindrical, head separated by constriction from rest of body, slightly less than $\frac{1}{4}$ total length. Dorsal plate situated posteriorly, slightly wider than rest of body, posterior margin variable, evenly rounded to very slightly bilobed. 1st antenna and bases of 2nd antenna dorsally visible. 1st antenna 7-segmented, terminal segment shortest, with 4 blunt spines. 2nd antenna 2-segmented, basal segment curved, tapering, terminal segment shorter, strongly falcate. 1st maxilla 3-segmented, terminal segment conical, basal segment with 2 broad spines distally. 2nd maxilla 3-segmented, terminal segment with 2 rows of blunt teeth and blunt spine on inner margin, middle segment with single distal spine. Maxilliped 2-segmented, basal segment broad, terminal segment shorter, tapering distally with falcate striated process and short blunt spine. 1st thoracic leg biramous, exopod of 1 segment, bearing 5 blunt distal spines, endopod of 1 segment, bearing elongate blunt distal spine. Tiny papilla-like process at base of endopod. 2nd thoracic leg biramous, exopod of 1 segment, bearing 4 short distal spines, tiny papilla bearing single

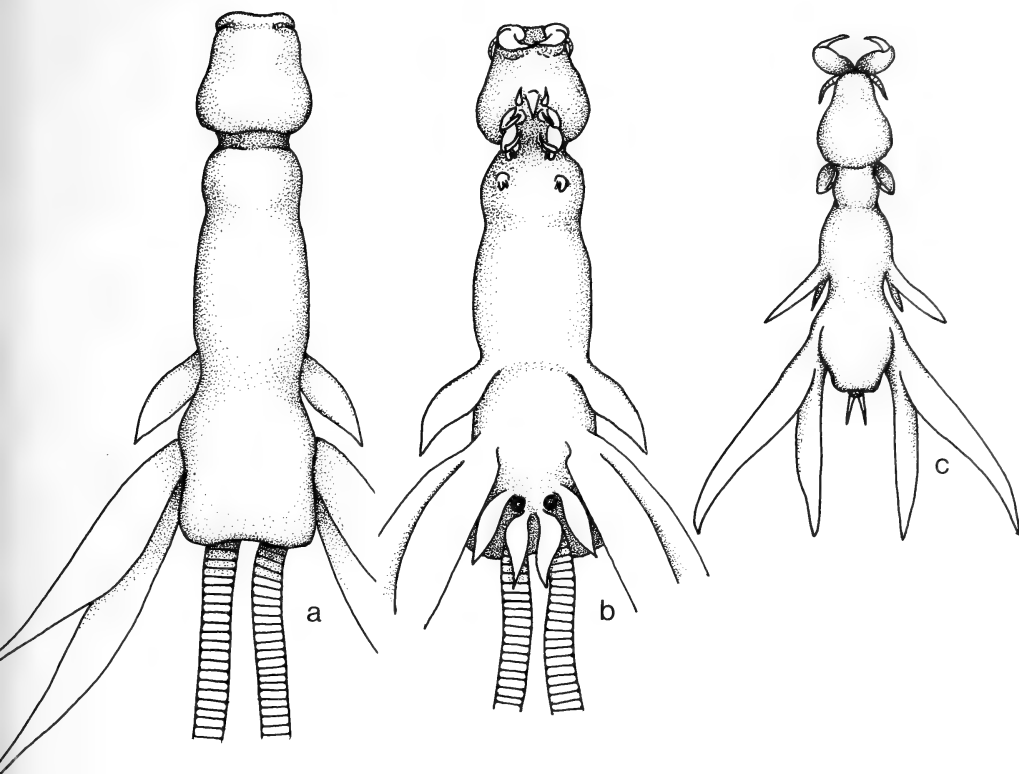


Fig. 19. *Lernanthropus ecclesi* n. sp. a. female in dorsal view; b. female in ventral view; c. male in dorsal view.

seta at base of exopod. Endopod of 1 segment, bearing single terminal spine. 3rd legs lamellar, uniramous, much shorter than 4th legs. Latter biramous, inner ramus slightly longer than outer, both lamellar with long tapering apex. 5th leg of single lamella, not dorsally visible. Caudal rami similar in form to 5th legs.

♂. Slightly more than $\frac{1}{2}$ length of ♀, body slender. 1st antenna dorsally visible, structure as in ♀. 2nd antenna 2-segmented, basal segment broadly tapering, with tiny spine on inner face near base, terminal segment short, with strong striated falcate distal process, and short blunt spine at midpoint. Mandible slender, apex with 7 denticles. 1st and 2nd maxilli and maxilliped as in ♀. 1st thoracic leg biramous, exopod of 1 segment, with 5 short distal spines. Endopod 1-segmented, with slender bristled seta, 2nd thoracic leg biramous, exopod distally expanded, bearing 3 submarginal spines, endopod shorter than exopod, armed with short bristles and terminal fringed seta. 3rd thoracic leg biramous, outer ramus about twice length of inner. 4th legs biramous, rami subequal, lamellar. 5th legs absent. Caudal rami short, slender.

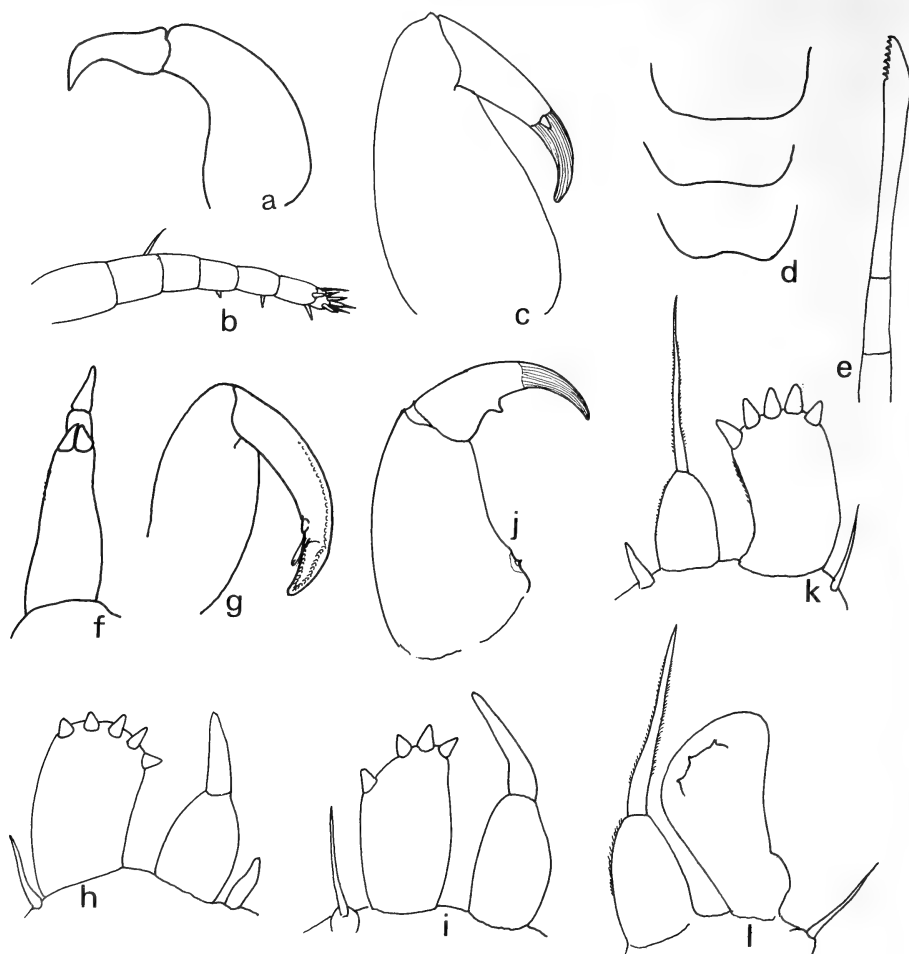


Fig. 20. *Lernanthropus ecclesi* n. sp. a. 2nd antenna, ♀; b. 1st antenna, ♀; c. maxilliped, ♀; d. 3 variations in the posterior margin of the dorsal plate, ♀; e. mandible; f. 1st maxilla; g. 2nd maxilla; h. 1st thoracic leg, ♀; i. 2nd thoracic leg, ♀; j. 2nd antenna, ♂; k. 1st thoracic leg, ♂; l. 2nd thoracic leg, ♂.

Material

9 ovigerous + 2 ♀♀, 5 with attached ♂♂ + 2 ♂♂, from yellowtail, *Seriola lalandi*, Kalk Bay. Holotype and allotype S.A.M. A13021, paratypes S.A.M. A13057. Total length ♀ 7,8 mm, ♂ 3,4 mm.

Remarks

Wilson (1932) described *Lernanthropus paenulatus* taken from *Seriola lalandi* from Woods Hole, U.S.A. Undoubtedly, the present material, taken from the same host, is closely related to Wilson's species, but some differences do exist. The female of *L. paenulatus*, at 9,5 mm, is somewhat larger than *L. ecclesi*

(6.9–7.3 mm), while the male (2.5 mm) is smaller (3.0–3.3 mm). The dorsal plate almost completely conceals the 4th legs in the American species while in the present material the 4th legs are dorsally conspicuously visible, while the tips of the 5th legs can also be seen. The 1st maxilla of the female of *L. ecclesi* is more slender, and armed with a single terminal and 2 subterminal spines, while in *L. paenulatus* the 1st maxilla has 2 terminal spines, plus another one third the length from the base. The 2nd leg of the female of *L. ecclesi* lacks the heel-like structure found in *L. paenulatus* while the male of the latter species lacks a spinose exopod, as found in *L. ecclesi*. These subtle differences may reflect differences within separate populations of the same species, or may indicate a specific separation. It would be of interest in this respect, to ascertain the amount of contact between the American and South African populations of the host species. Until more material becomes available, it would seem best to separate the present species.

***Lernanthropus sarbae* n. sp.**

(Figs 21a–c, 22a–i)

Description

♀. Head $\frac{1}{4}$ total length. 2nd thoracic segment forms 'neck'. 3rd thoracic segment fused with 4th and genital segment, segments indicated by slight lateral indentations. Dorsal plate forms large almost circular shield posteriorly. Genital segment with small lateral knob at point of attachment of egg sacs. Abdomen small, rounded. 1st antenna dorsally visible, indistinctly 7-segmented, with 8 or 9 terminal setae. 2nd antenna 2-segmented, basal segment about twice length of terminal segment, broadly tapering, terminal segment short, with stout striated apical process. 1st maxilla bilobed, inner lobe short, with single terminal spine, outer lobe elongate, with 2 terminal spines. 2nd maxilla 3-segmented, terminal segment short, armed with numerous spines, median segment slender, with single distal spine. Maxilliped 2-segmented, basal segment with tiny spine on inner surface, distal segment short, with hooked terminal process. 1st leg biramous, exopod consisting of single segment with 5 strong terminal spines, endopod of single segment and distal bristled spine, short setose process at base. 2nd leg biramous, exopod of single segment with 4 distal spines, endopod of single segment. 3rd legs lamellar, curved ventrally. 4th legs consisting of 2 elongate slender processes, fused basally for short distance. 5th leg consisting of tiny digitiform process. Caudal rami short, tapering.

♂. Slightly shorter than ♀, head about $\frac{1}{3}$ total length. 1st antenna as in ♀. 2nd antenna 2-segmented, basal segment broadly tapering, with 2 blunt processes on inner surface near base. Distal segment short, with strong striated falcate process terminally, and short spine on inner margin. 1st and 2nd maxilli as in ♀. Maxilliped 2-segmented, basal segment broad, with tiny spine

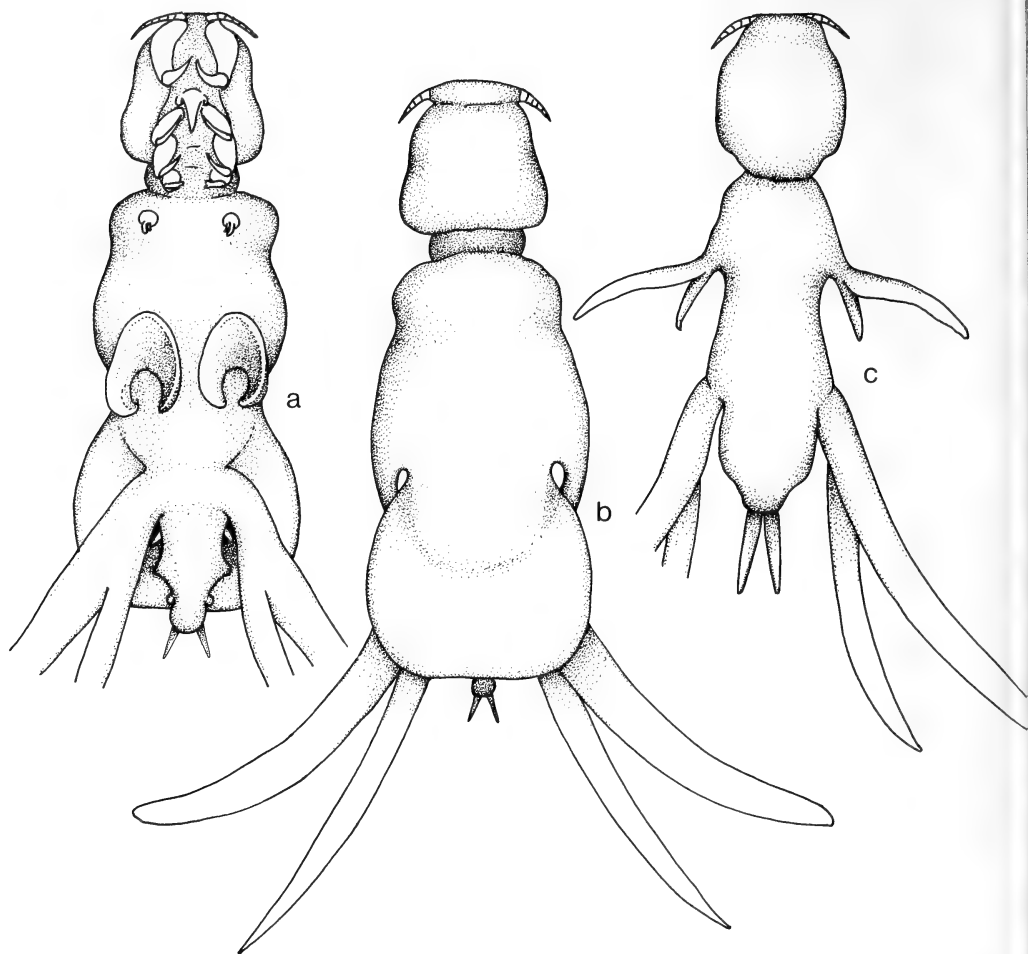


Fig. 21. *Lernanthropus sarbae* n. sp. a. female in ventral view; b. female in dorsal view; c. male in dorsal view.

on inner margin, terminal segment short, with curved striated distal process, with short spine on inner margin. 1st thoracic leg as in ♀. 2nd thoracic leg biramous, exopod somewhat expanded, endopod of single tapering bristled segment, bearing short terminal seta. 3rd thoracic leg situated laterally, biramous, inner ramus shorter than outer. 4th legs as in ♀. Caudal rami elongate, almost equal in length to genital segment and abdomen.

Material

1 ovigerous + 1 ♀, 1 ♂, from *Rhabdosargus sarba*, Durban. Holotype and allotype S.A.M. A13020, paratype S.A.M. A13056. Total length ♀ 3.0 mm, ♂ 2.1 mm.

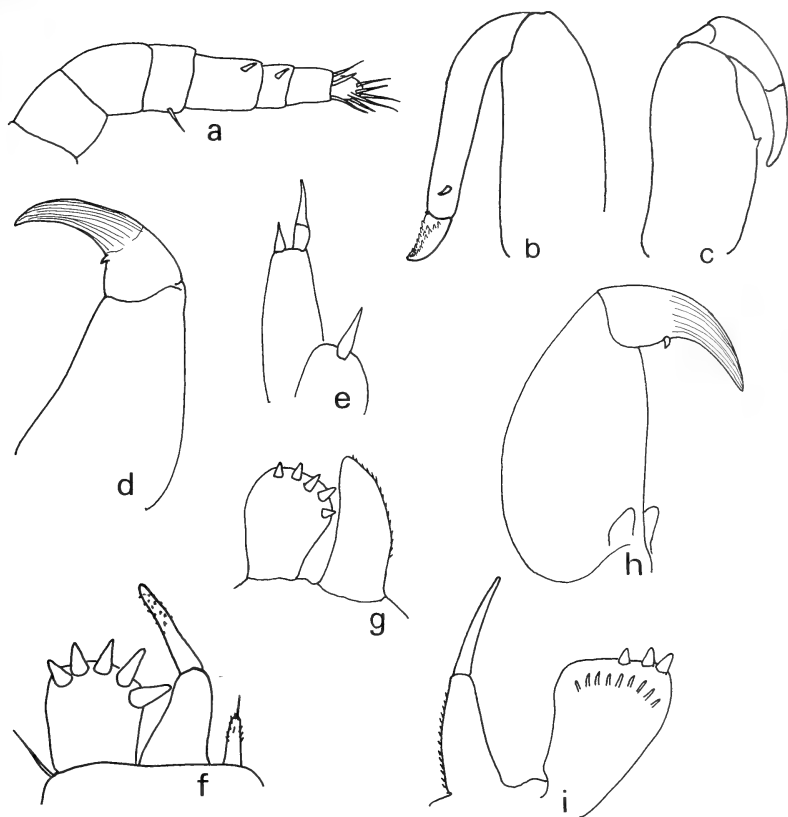


Fig. 22. *Lernanthropus sarbae* n. sp. a. 1st antenna, ♀; b. 2nd maxilla, ♀; c. maxilliped, ♀; d. 2nd antenna, ♀; e. 1st maxilla, ♀; f. 1st thoracic leg, ♀; g. 2nd thoracic leg, ♀; h. 2nd antenna, ♂; i. 2nd thoracic leg, ♂.

Remarks

The present species falls into the group characterized in the female by the possession of a large almost circular extension of the dorsal plate, the curved lamellar 3rd legs, and very elongate rami of the 4th legs, which are fused basally for a short distance. This group includes *L. amplitergum* Pearse, *L. kroyeri* Van Beneden, *L. giganteus* Krøyer, *L. chrysophrys* Shishido, *L. latis* Yamaguti, *L. eddiwarneri* Delamare-Deboutteville & Nunés-Ruivo, *L. rathbuni* Wilson, and *L. opisthopteri* Pillai.

L. amplitergum differs from the present species in the possession of a posteriorly notched dorsal plate in the female, while the 3rd legs of the male have both rami of equal length. *L. kroyeri* possesses a more rounded cephalothorax than the present species, and the rami of the 4th legs in both the female and male relatively shorter. *L. giganteus* in the female possesses dorso-lateral extensions of the dorsal plate, above the bases of the 3rd legs. The 3rd legs of the

male have the rami very unequal, the inner one being a mere papilla. *L. chrysophrys* is very similar to the present material, but has postero-lateral extensions of the cephalic shield, and a 2nd maxilla rather more spinose.

L. latis in the female has the rami of the 4th legs relatively shorter than in the present species, and these possess at their tips a spine-covered knob. In the male, the 3rd and 4th legs are relatively shorter and also possess spinose apices. There is also a considerable difference in size between the species.

L. eddiwarneri in the female possesses a more squat body than in the present species, and a posteriorly notched dorsal plate, while the abdomen is not dorsally visible.

L. rathbuni in the female has a distal spine on the penultimate segment of the 2nd maxilla and relatively stout caudal rami, and the inner ramus of the 1st legs armed with bristles.

L. opisthopteri in the female is a squatter animal and has the carapace extended forward to form 2 rounded lobes. The 4th legs are more slender than the present species while the 2nd antenna possesses 3 spines, and the 2nd maxilla possesses 2 spines on the middle segment, unlike the present species.

Family **Eudactylinidae**

Kroyeria carchariaeglauci Hesse

(Fig. 23a-c)

Kroyeria carchariaeglauci: Delamare-Deboutville & Nunés-Ruivo, 1953: 209, fig. 4
Yamaguti, 1963: 162, pl. 187, fig. 2.

Material

15 ovigerous ♀♀ + 4 ♂♂ from *Prionace glauca*, False Bay.
Total length ♀ 6.3 mm, ♂ 5.5 mm.

Previous records

From *Prionace glauca* W. Pacific, Mediterranean, N.E. America, and from *Carcharias milberti* and *Galeus glaucus*, Martha's Vineyard, N.E. America.

Remarks

The present material agrees well with the above descriptions and figures; the only detectable difference is that the abdomen is not obviously segmented.

Nemesis lamna Risso

(Fig. 24)

Nemesis lamna: Wilson, 1932: 461, pl. 32. Yamaguti, 1963: 167.

Description

♀. Body elongate, cephalothorax longer than broad, with lateral indentations. 4 free thoracic segments more or less of equal length and breadth, with deep gaps between them. Genital segment broader than long, about one-fifth

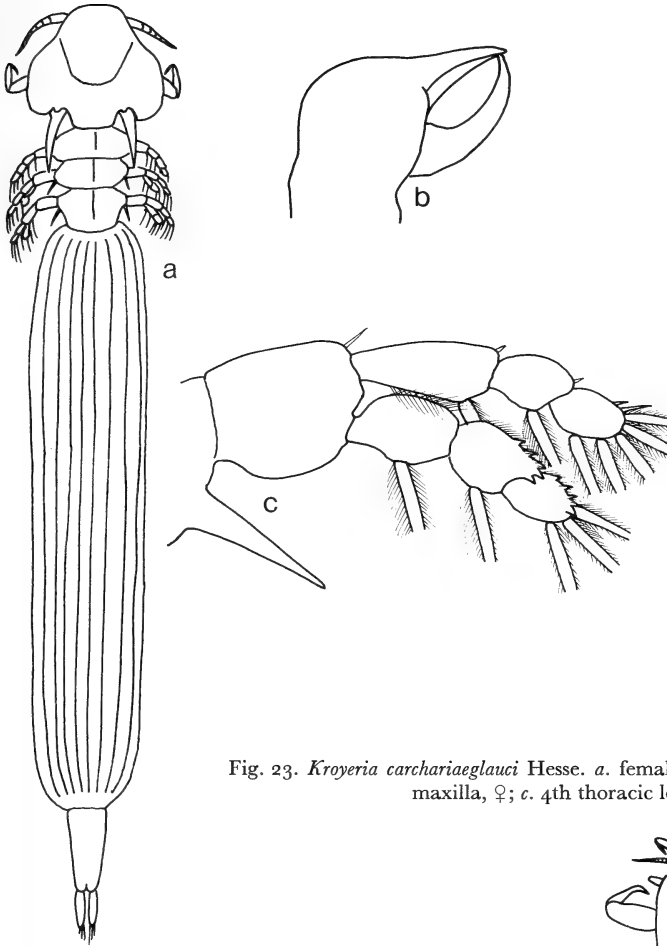


Fig. 23. *Kroyeria carchariaeglauci* Hesse. a. female in dorsal view; b. 2nd maxilla, ♀; c. 4th thoracic leg, ♀.

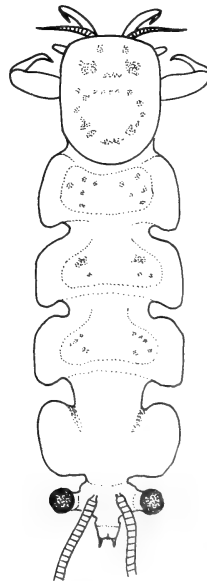


Fig. 24. *Nemesis lamna* Risso. Female in dorsal view.

length of preceding free thoracic segment. Abdomen 2-segmented, distal segment longer than proximal segment. Spermatophores spherical, almost black.

Material

Numerous ovigerous ♀♀, length up to 11 mm, from gills of *Carcharodon carcharias* from False Bay, Cape.

Previous records

From Mediterranean, eastern U.S.A., California, Japan, Argentina, on sharks of the genera *Alopias*, *Carcharias*, *Carcharodon*, *Cetorhinus*, *Isurus*, *Odontaspis*, and *Oxyrhina*.

Remarks

The greater length, the very obvious lateral indentations, and the width of the 5th free segment immediately distinguish this species from *N. pallida*, the other species recorded from this area.

Family **Pseudocycnidae**

***Pseudocycnoides rugosa* n. sp.**

(Figs 25*a, b*, 26*a-i*)

Description

1st thoracic segment fused with carapace. Latter shield-like, anteriorly narrowed, 1st antenna dorsally visible. 2nd thoracic segment well-defined, 3rd and 4th segments less-well defined, fused with genital segment. 2nd, 3rd and 4th segments each with blunt lateral process. 5th segment indicated only by single lateral seta. Genital segment cylindrical, 5 times longer than wide. Abdomen short, bearing blunt distal spine. 1st antenna 9-segmented, with large blunt spine on 3rd segment. 2nd antenna 3-segmented, terminal segment strongly hooked, bearing proximally a small hook, and single strong median spine. Oral tube conical, flanked by 1st maxillae. Latter 2-segmented, terminal segment spine-like, base rounded. 2nd maxilla exterior to 1st maxilla, 3-segmented, basal segment broad, twice thickness of median segment, latter distally curved, terminal segment short, serrate. Maxilliped 2-segmented, basal segment very broad, roughly oval, outer surface rugose, bearing fleshy rugose process anteriorly, terminal segment slender, strongly hooked, folding against inner surface of fleshy process of basal segment. 2nd thoracic segment with dorso-lateral rounded fleshy process, ventral to which, a large rounded lobe, somewhat rugose, bearing tiny lobe medially. Latter bears 2 single segments representing biramous leg. Outer ramus of latter bearing 2 short terminal spines, inner bearing 2 curved spines. 3rd thoracic segment similar to 2nd, but rudimentary leg uniramous, bearing strong terminal spine, plus

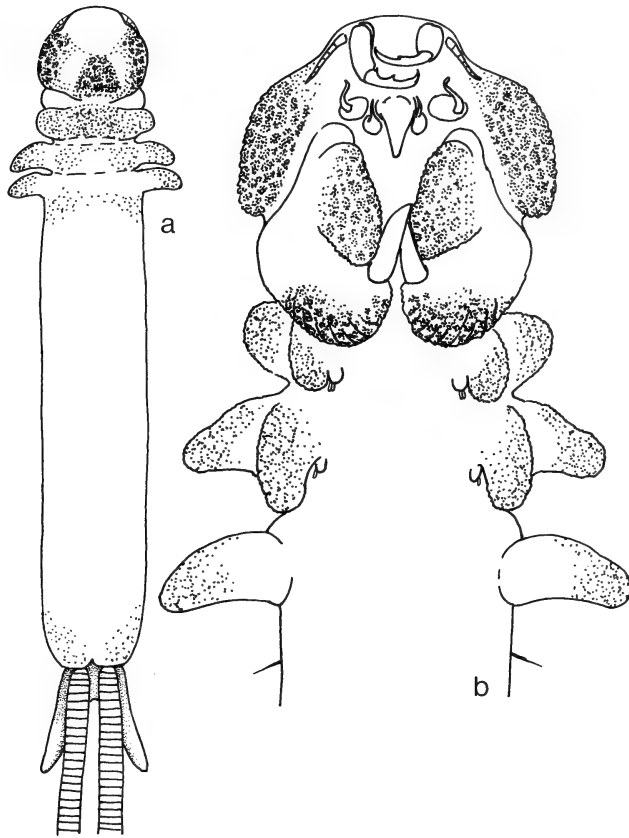


Fig. 25. *Pseudocycnoides rugosa* n. sp. ♀. a. female in dorsal view; b. anterior region of female in ventral view.

2 more slender spines. No trace of 4th legs, 4th thoracic segment marked by dorso-lateral process.

Material

4 ovigerous ♀♀ from *Scomberomorus maculatus* gills, Durban. Holotype S.A.M. A13058, paratypes S.A.M. A13059. Total length ranging from 5.5 mm to 6.0 mm. Colour red when fresh.

Remarks

The following characteristics of the female place the present material in the genus *Pseudocycnoides*: Head fused with 1st thoracic segment, 2nd thoracic segment free, 3rd and 4th segments fused with genital segment, marked by lateral digitiform processes, basal segment of maxilliped with large fleshy process, 1st thoracic legs very reduced, biramous, 2nd legs uniramous, 3rd legs lacking. Two species of this genus have been described, viz. *P. scomberomori* (Yamaguti 1939), and *P. armata* (Bassett-Smith 1898).

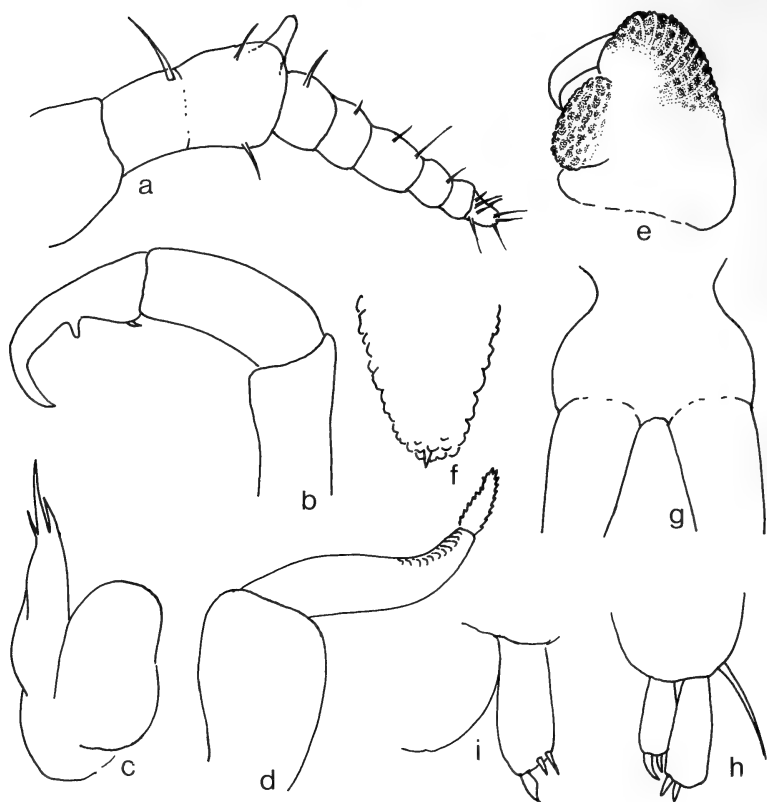


Fig. 26. *Pseudocycnoides rugosa* n. sp. ♀. *a.* 1st antenna; *b.* 2nd antenna; *c.* 1st maxilla; *d.* 2nd maxilla; *e.* maxilliped; *f.* apex of caudal ramus; *g.* abdomen; *h.* 1st thoracic leg; *i.* 2nd thoracic leg.

P. armatus possesses a 6–7 segmented 1st antenna which lacks a proximal process, whereas the present species has an 8–9 segmented 1st antenna with proximal process. The former species possesses a slightly rugose maxilliped, with a tooth on the inner margin of the terminal segment, and a small fleshy process on the basal segment. The present species has a very rugose maxilliped, lacks the tooth on the terminal segment, and has a much larger fleshy process.

Family **Lernaeoceridae**

Lernaeeniscus gonostomae n. sp.

(Fig. 27*a–h*)

Description

Head with 2 lateral unbranched horns, each with bulbous base, tapering, curved, apically pointed. Proboscis large, cylindrical, springing from bases of horns, dorsally with 1st and 2nd antennae, distally narrowed. 1st antenna

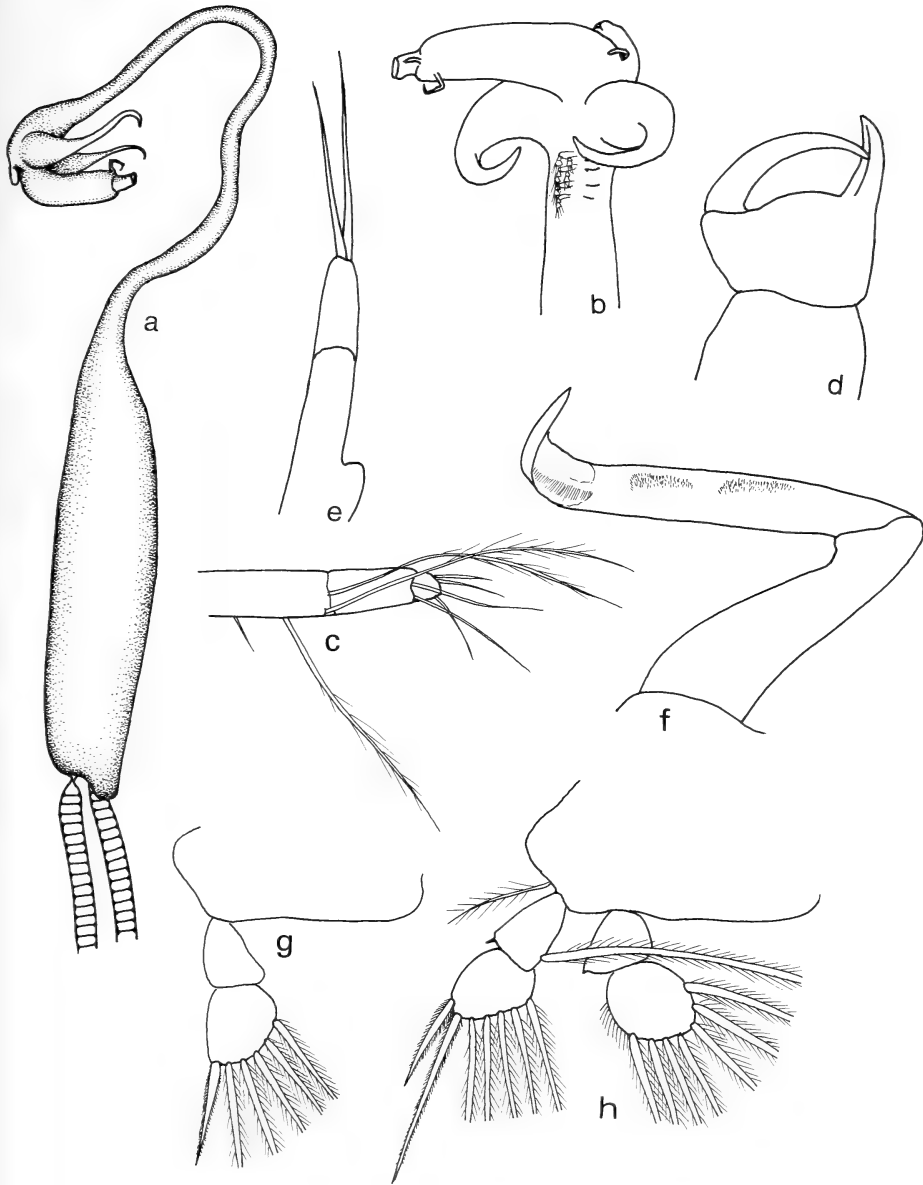


Fig. 27. *Lernaeniscus gonostomae* n. sp. ♀. a. female; b. head region further enlarged; c. 1st antenna; d. 2nd antenna; e. 1st maxilla; f. 2nd maxilla; g. 3rd thoracic leg; h. 1st thoracic leg.

indistinctly segmented, bearing several elongate plumose setae, 2 of which longer than appendage itself. 2nd antenna 2-segmented, apically strongly chelate. 1st maxilla simple, 2-segmented, with 2 terminal setae. 2nd maxilla indistinctly 3-segmented, terminally with flattened hook bearing fine striations on inner surface. Median segment with 2 patches of very fine setae. 4 pairs

of thoracic legs present on ventral surface just below horns. 1st 2 pairs biramous, posterior 3 pairs uniramous. 1st and 2nd thoracic legs with broad protopodite, exopod 2-segmented, basal segment with single plumose seta on inner margin, distal segment with 2 fringed spines and 5 plumose setae. Endopod 2-segmented basal segment unarmed, distal segment with 7 plumose setae. 3rd and 4th thoracic legs uniramous, rami 2-segmented, distal segment with 5 plumose setae and single fringed spine. Neck equal in length to slightly longer than trunk, buried to its base in host, cylindrical. Trunk more or less cylindrical, with very short abdominal region. Egg sacs elongate.

Material

3 ovigerous ♀♀ from mesopelagic *Gonostoma elongatum*, 26° 30' S, 33° 40' E. Holotype S.A.M. A11751, paratypes S.A.M. A13031, A13173. Length of trunk 8,5–10,8 mm; neck length approximately 11,0–14,0 mm.

Remarks

As several descriptions and figures of species described in the nineteenth century are not available, new specific status is given the present species with some trepidation. *L. cerberus* Leigh-Sharpe possesses horns similar to the present species, but also has a blunt dorsal horn not found in the present species. *L. gonostomae* closely resembles *L. spratta* (Sowerby) but does not possess a moniliform neck region, while the proboscis is much larger than in the latter species. *L. radiatus* (Le Sueur) is variable with regard to the number of horns, and has been recorded with 2 (Wilson 1917: 60). These horns, however, are blunt, as they are not used for actual attachment, but merely for anchoring. Several other differences, including the length of the abdominal region, the segmented nature of the 1st antenna, and the maxilliped separate *L. radiatus* from the present material.

L. anchoviellae Sebastian & George, 1964, resembles the present species to some extent. The 'neck' of the former species, however, is longer, compared to the length of the trunk, while the head possesses 2 blunt postero-dorsal horns, rather than the 2 tapering and more elongate horns of *L. gonostomae*. The abdominal region of the latter is hardly developed, while *L. anchoviellae* possesses a moderately elongate and tapering 'abdomen'.

Peniculisa furcata (Krøyer)

(Fig. 28a-e)

Peniculisa furcata: Leigh-Sharpe, 1934: 28, fig. 26. Shiino, 1956: 602. Yamaguti, 1963: 203, pl. 224, fig. 3.

Description

Body elongate, cephalothorax oval, irregular band of black pigment stretching from cephalothorax, through trunk, into posterior processes. 2nd antenna stout, bearing strongly curved hook shielded by disc-like expansion.

Maxilliped 3-segmented. Four pairs of thoracic legs present, first 3 pairs dorsally visible, 4th pair at proximal end of genital segment. Each leg very reduced, consisting of single short lobe folded on itself with minute hook at apex. Genital segment bearing 2 elongate parallel processes, at least two-thirds length of trunk. Abdomen very short with rounded posterior processes. Caudal rami consisting of minute laminae bearing 4 short setae. Trunk with short lobe ventrally, at base of elongate processes. Egg sacs originate just below short lobes.

Material

6 ovigerous + 1 non-ovigerous ♀♀, length range from 2,1 mm to 3,0 mm. On *Paramonacanthus barnardi*, Inhaca Island, Moçambique.

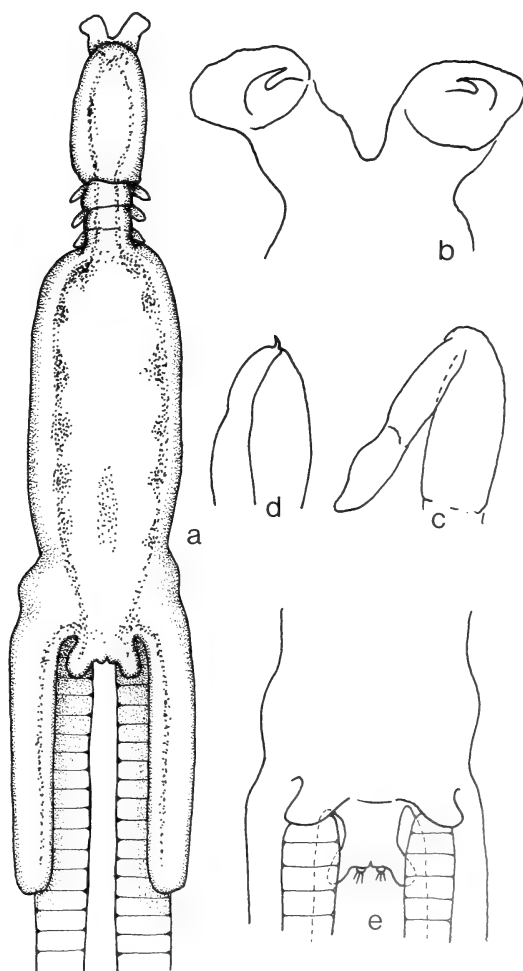


Fig. 28. *Peniculisa furcata* (Krøyer).
a. female in dorsal view; b. 2nd antenna, ♀; c. maxilliped, ♀; d. 1st thoracic leg, ♀; e. genital segment and abdomen in ventral view, ♀.

Previous records

On *Ostracion punctatus*, from Indonesia. On *Holacanthus* sp., from Indian Ocean. On *Tetrodon* sp., from Ceylon.

Remarks

The present material differs from descriptions of *P. furcata* only in the possession of the short ventral lobes and the tiny hook at the base of the legs.

Family **Pennellidae***Pennella* sp.*Material*

Numerous ♀♀, from Sei, Fin, and Sperm whales from Donkergat Whaling Station, Saldanha Bay.

Remarks

Most of the present material possesses 3 horns, of varying length, on the head. The head in most cases agrees well with the figures given by Delamare-Deboutteville & Nunés-Ruivo (1953) and Barnard (1955a) for *P. crassicornis*. The proportion of head length to trunk length is also very variable. In some specimens the neck is about $1\frac{1}{2}$ times the trunk length, while in others it is up to twice the length of the neck. Using the characters given by Wilson (1917) some of these specimens would agree with *P. balaenopterae*, while others would agree with *P. crassicornis*.

A morphometric study of this collection was made in collaboration with Dr P. Best, who collected the specimens. The total length and the lengths of the lateral and nuchal horns, neck, trunk, abdomen, and egg strings were measured. The material appeared to separate into groups but with considerable overlap between them. The groups did not appear to be related either to the variations of head morphology or to the species of their host. Type specimens of species described by Quido were borrowed from the Paris museum for comparison but they could not be satisfactorily related to the present material. No specific status will be given to the present material until a reliable method of distinguishing the species has been established.

Order LERNAEOPODOIDA

Family **Lernaeopodidae***Brachiella lithognathae* n. sp.

(Fig. 29a-g)

Description

♀. Cephalothorax slender, elongate, with slight bulge at base on either side. 1st antenna 4-segmented, terminal segment bearing 3 spines and a blunt projection. 2nd antenna biramous, outer ramus overhangs inner, apically

rounded and slightly roughened. Inner ramus 2-segmented, apically bearing rounded lobe armed with minute spines, and cluster of 6 large spines. 1st maxilla distally with 2 lobes each bearing stout seta. Palp short, bearing 2 stout seta. Mandible with 6 teeth. Maxilliped apically with strong claw and strong subapical claw, spinose pad on basal segment. 2nd maxillae stout, about one-quarter length of cephalothorax, separate, fused at tips. Trunk roughly rectangular, genital process a rounded papilla. 2 small posterior processes present.

♂. Cephalothorax with carapace much shorter than trunk, latter broadly rounded, 2nd maxilla and maxilliped large, prehensile. Length 0,6 mm.

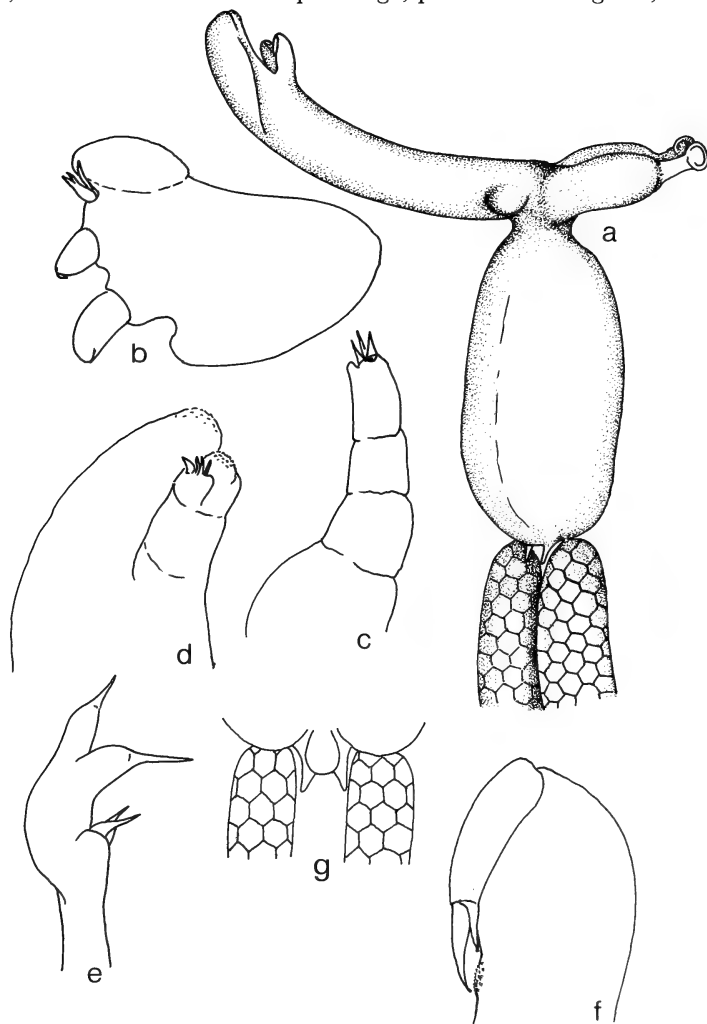


Fig. 29. *Brachiella lithognathae* n. sp. a. female; b. male; c. 1st antenna, ♀; d. 2nd antenna, ♀; e. 1st maxilla, ♀; f. maxilliped, ♀; g. posterior genital segment in ventral view, ♀.

Material

2 ovigerous ♀♀ from *Lithognathus lithognathus*, Milnerton, Cape. 3 ovigerous ♀♀ from *Lithognathus aureti*, Rocky Point, S.W.A. Holotype and allotype S.A.M. A13030, paratypes S.A.M. A13060, A11792.

Remarks

Of the species of *Brachiella* possessing a relatively elongate cephalothorax and 2 tiny posterior processes on the trunk, the present species most closely resembles *B. exigua* Brian, recorded from *Pagellus erythrius* from the Mediterranean, from *Dentex vulgaris* from Mauritania, and from *Merluccius* sp. from the Dry Tortugas. The most obvious differences between these 2 species lies in the size, as the table illustrates. Further differences exist in the 2nd antennae, which in the present species is not as spinose distally as in *B. exigua*, and in the maxilliped which lacks the strong subapical spination of *B. exigua*.

		<i>B. exigua</i>	<i>B. lithognathae</i>
cephalothorax	..	1,90 mm	4,0 mm
trunk	1,47 mm	3,0 mm
egg sacs	1,90 mm	5,2 mm
Dimensions for <i>B. exigua</i> taken from Nunés-Ruivo (1954).			

Lernaeopoda etmopteri Yamaguti

(Fig. 30a-f)

Lernaeopoda etmopteri Yamaguti, 1939: 549, pl. 44, figs 104-106. Shiino, 1956: 275, figs 4, 5.

Description

Cephalothorax with dorsal carapace, short, in line with trunk. Latter pear-shaped, $3\frac{1}{2}$ -4 times length of cephalothorax. No distinct neck. No genital process, but 2 sausage-shaped posterior processes present, with a pair of tiny spiniform processes between them. 1st antenna 4-segmented, with 4 terminal setae. 2nd antenna biramous, outer ramus distally rounded, inner ramus indistinctly 2-segmented, distally bilobed, both lobes bearing spines. Mandible with 7 teeth. 1st maxilla distally trilobed, each lobe ending in single stout seta, palp some way below trilobed apex, bearing 3 spines. 2nd maxilla very elongate slender, twice length of trunk, corrugated, distally fused only at tips, bulla small. Maxilliped strongly subchelate, apex strongly hooked, inner margin of basal segment with large finely spinose pad distally, smaller spinose pad proximally, and short spine.

Material

2 ovigerous ♀♀ (one with posterior processes detached) from shark, *Etmopterus* sp., taken west of Cape Point, in 450 metres. Length of cephalothorax + trunk 12,6 mm, 8,0 mm. Length of 2nd maxilla 22,0 mm, 8,0 mm.

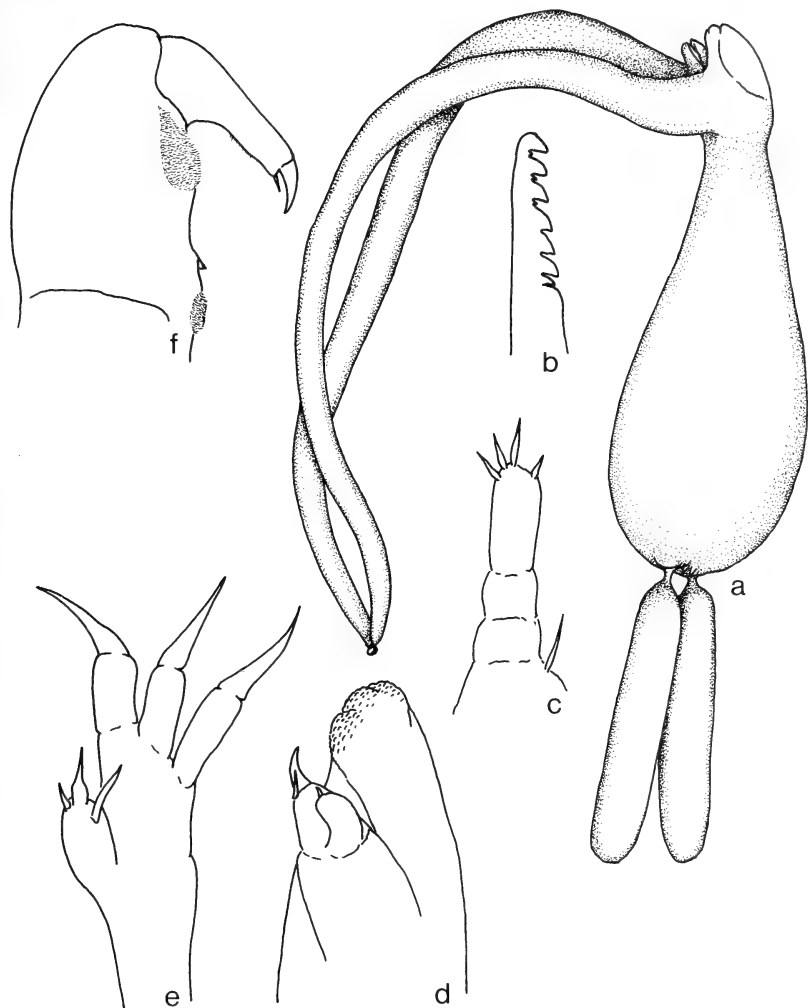


Fig. 30. *Lernaepoda etmopteri* Yamaguti. a. female; b. mandibular apex; c. 1st antenna, ♀; d. 2nd antenna, ♀; e. 1st maxilla, ♀; f. maxilliped, ♀.

Previous records

On *Etmopterus lucifer*, from Japan.

Remarks

The present material agrees well with both Yamaguti's and Shiino's descriptions, especially with regard to the appendages. Slight differences do exist. The 2nd maxilla of the present material is far more elongate than that figured by Shiino. The Japanese material, however, is described as wrinkled;

possibly the 2nd maxillae were contracted, while in the present material they are fully relaxed. The somewhat lobose appearance of the trunk as figured by Shiino may also be due to contraction.

Schistobranchia ramosa (Krøyer)

(Fig. 31)

Schistobranchia ramosa (Krøyer), Kabata, 1964: 99.

Charopinus ramosus: Scott & Scott, 1913: 191, pl. 55, figs 6, 7. Yamaguti, 1963: 253, pl. 272, fig. 3.

Material

3 ovigerous ♀♀ from *Raia batis*, Table Bay. Total length approximately 9,0 mm.

Previous records

On *Raia clavata* and *R. maculata*, from Irish and North Sea. On *R. radiata* from Iceland and Barents Sea. On *R. scabrata* from Canada.

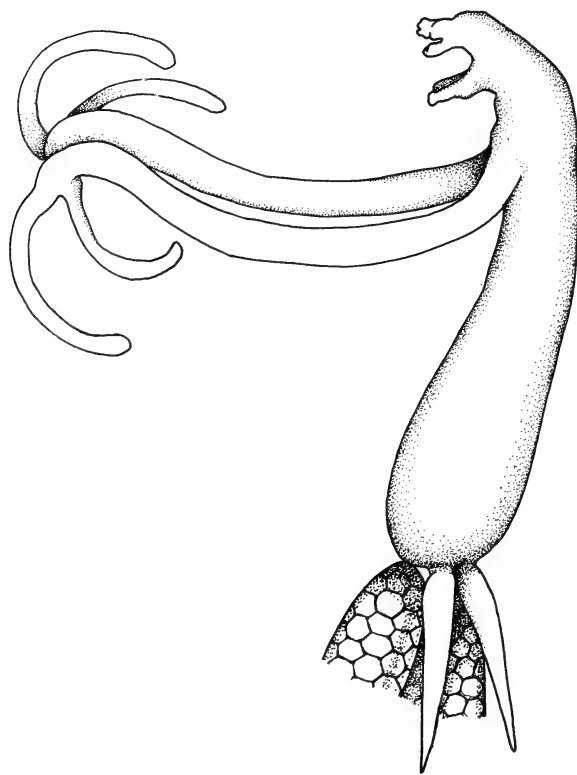


Fig. 31. *Schistobranchia ramosa* (Krøyer). Female.

Remarks

The 2nd maxillae, which are distally fused, and each split into 2 slender 'fingers' easily identify this species. This would seem to be the first record of the species from the Southern Hemisphere.

Clavellisa cf. *ilishae* Pillai

(Fig. 32a-f)

Description

Cephalothorax extremely elongate, slender, of uniform thickness. Trunk regularly oval, twice as broad as long. 1st antenna indistinctly 3-segmented, armed with 7 setae. 2nd antenna biramous, outer ramus broadly rounded, bearing 3 setae, inner ramus shorter and more slender than outer, with 4

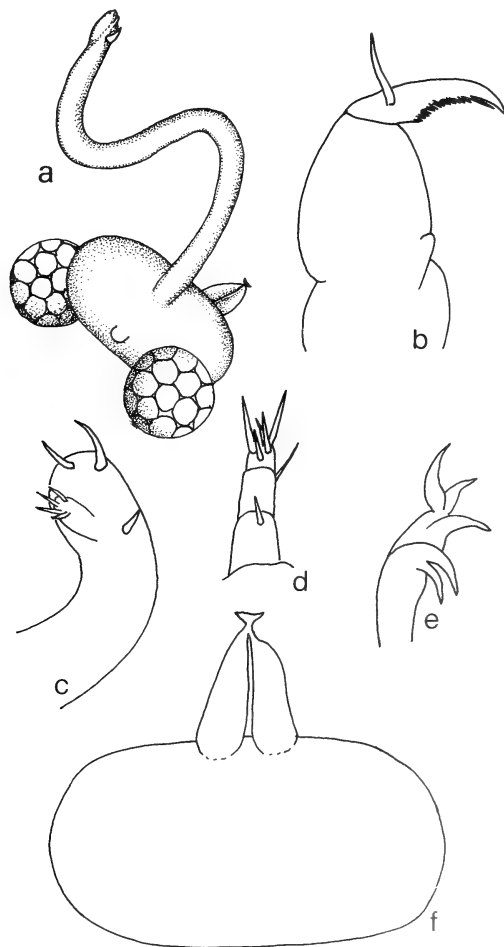


Fig. 32. *Clavellisa* cf. *ilishae* Pillai. a. female; b. maxilliped, ♀; c. 2nd antenna, ♀; d. 1st antenna, ♀; e. 1st maxilla, ♀; f. trunk and 2nd maxillae, ♀.

apical setae. 1st maxilla with 3 terminal curved spines, palp with 2 curved spines. 2nd maxillae springing from trunk, some distance from base of 'neck', separate, but apically fused into bulla. Maxilliped 2-segmented, terminal segment curved, with strong apical hook and numerous short spines on inner margin, bearing one strong seta. Egg sacs globular, with small prominence between them, representing fused anal laminae.

Material

3 ovigerous ♀♀ from gills of *Sardinops ocellata*, False Bay.

Dimensions: breadth of trunk	..	1,0 mm	0,8 mm	0,8 mm
egg sacs	..	0,4 mm	0,3 mm	0,3 mm
cephalothorax length		2,0 mm	2,5 mm	1,5 mm

Remarks

The present material closely resembles *C. ilishae* described from *Ilisha filigera* and *Euplatygaster indica* from India. The dimensions and appendages agree well with Pillai's description (1962:79), while a few differences do exist. The egg sacs of the present material are spherical, while *C. ilishae* possesses pyriform sacs. The present material also lacks the 2 pairs of tubercles, each bearing a seta, on the anterior border of the trunk, as well as the cylindrical process adjacent to the anal laminae. These differences hardly seem to warrant the erection of a new species.

Clavellopsis appendiculata Kirtisinghe

(Fig. 33a-c)

Clavellopsis appendiculata Kirtisinghe, 1950: 84, figs 40-43. Pillai, 1968b: 129, figs 7, 8.

Isobranchia appendiculata Heegaard, 1947: 239, figs 1-4. Yamaguti, 1963: 260, pl. 287, fig. 1.

Description

♀. Cephalothorax cylindrical, elongate, dorsally flexed. 2nd maxillae completely fused, bulla cup-like. Trunk pear-shaped, slightly dorso-ventrally flattened. 2 dorsal posterior processes situated laterally, 2 ventral processes situated closer to midline. 1st antenna 4-segmented, bearing 3 terminal setae and single short spine. 2nd antenna biramous, outer ramus apically rounded, inner ramus of 1 segment with single apical spine. Maxilliped subchelate, with strong terminal hook-like claw, and serrated region on inner basal area. Basal segment with short spine on inner margin.

♂. 1st antenna 3-segmented, with 3 terminal setae and 1 short spine. 2nd antenna biramous, inner ramus 4-segmented, terminal segment with large curved spine, smaller accessory spine, and row of tiny curved spines. Outer ramus indistinctly 3-segmented, terminal segment rounded, bearing single short spine.

Material

2 ovigerous ♀♀, 1 ♂ from *Chirocentrus dorab*, Durban. ♀ length cephalothorax 2,0 mm, length trunk + posterior processes 3,6 mm.

Previous records

From *Chirocentrus dorab*, Iranian Gulf.

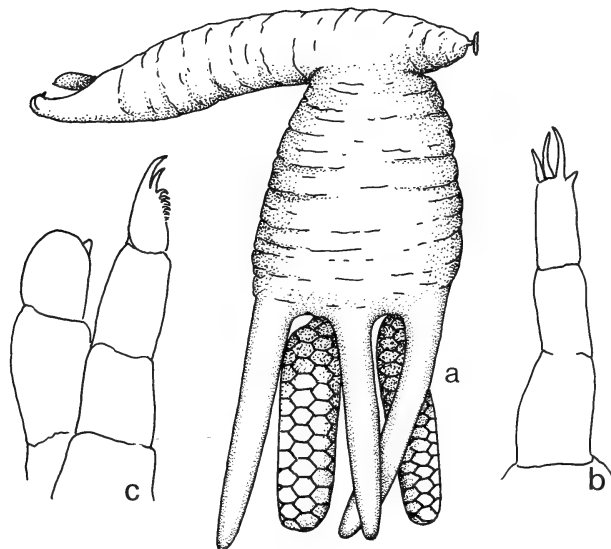


Fig. 33. *Clavellopsis appendiculata* Kirtisinghe. a. female; b. 1st antenna, ♂; c. 2nd antenna, ♂.

Family **Naobranchiidae*****Naobranchia pritchardae* n. sp.**

(Fig. 34a-c)

Description

Cephalothorax elongate, slender, only slightly longer than distance from base of cephalothorax to tip of egg sacs. Head demarked by slight constriction. 1st antenna indistinctly 3-segmented with stout apical spine. 2nd antenna bilobed, each ramus consisting of single segment with distal spine. Maxilliped 2-segmented, terminal segment a strong curved hook with accessory spine and tiny spine near base. Buccal cone flanked by rounded striated process. Egg sacs lateral, trunk broad, each side with 3 slender elongate processes embracing egg sacs, 1 dorsal pair, 1 ventro-lateral pair, 1 ventral pair. Egg sacs extend both anterior and posterior to oviduct. Abdomen with single pair of slender caudal rami, enclosed in membranous sac, which also encloses egg sacs and trunk processes. Abdomen situated at about midpoint of length of egg sacs,

deep notch between latter. 2nd maxillae form 2 basally fused bands, on ventral surface of trunk.

Material

2 ovigerous ♀♀, from *Pomadasys operculare*, Durban. Holotype, S.A.M. A13042, paratypes S.A.M. A13063. Total length 4.0 mm, cephalothorax length 2.0 mm.

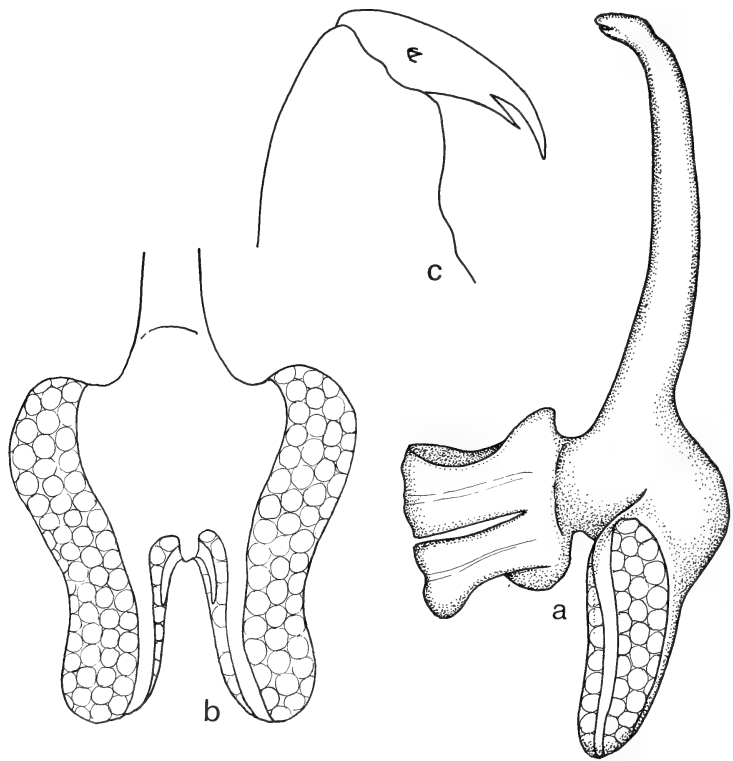


Fig. 34. *Naobranchia pritchardae* n. sp. a. female in lateral view; b. dorsal view of trunk, ♀; c. maxilliped, ♀.

Remarks

Of the 15 known species of the genus *Naobranchia*, the present material most closely resembles three species described by Nunés-Ruivo, in 1963, viz. *N. pagelli*, *N. sargi* and *N. smaridis*. These three species from West Africa, as with the present species, possess 3 pairs of processes on the trunk. *N. pagelli*, does not possess a posterior notch between the egg sacs, and is about twice the length of the present species. Neither *N. sargi* nor *N. smaridis* was an ovigerous specimen, and the presence or absence of a posterior notch can thus not be

determined. Neither possesses the strong 'shoulders' of *N. pritchardae*, while both are somewhat larger than the latter. They also differ in general proportions. *N. smaridis* has a cephalothorax about twice the length of the trunk, *N. sargi* $1\frac{1}{2}$ times the length of the trunk, while in the present species the cephalothorax is less than $1\frac{1}{2}$ times the length of the trunk.

The species is named for Dr Mary-Lou Pritchard of the University of Nebraska, who collected it, along with numerous other parasitic copepods, for the South African Museum.

Family Sphyriidae

Lophoura elongata n. sp.

(Fig. 35a-d)

Description

Cephalothorax very elongate, narrow. Neck shorter than cephalothorax, but of same thickness, bearing lobed and knobbed process distally. Genital segment flask-shaped, bearing posteriorly a median raised process flanked by oviduct openings. Single pair of processes bearing numerous sausage-shaped lobes attached medially to oviducal openings.

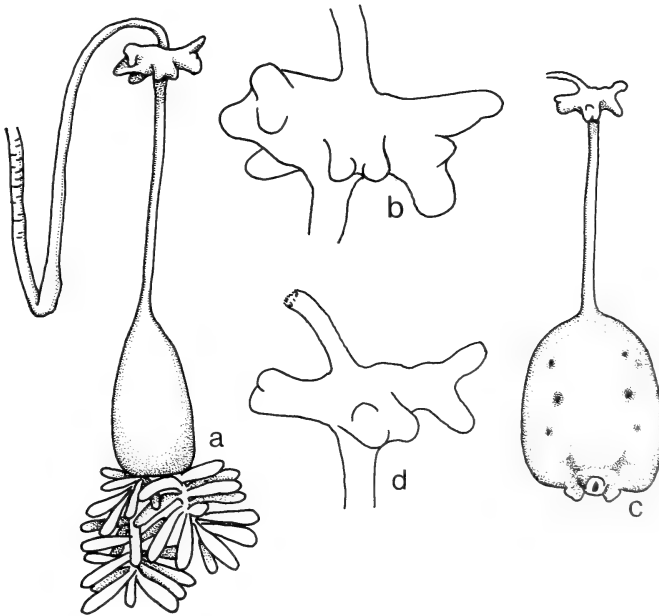


Fig. 35. *Lophoura elongata* n. sp. a. female, specimen A; b. lobed process further enlarged; c. female, specimen B; d. lobed process further enlarged.

Material

2 ♀♀ from *Synaphobranchus bathybius*, off Cape Point. Cephalothorax apex missing in both cases. Holotype S.A.M. A11802, paratype S.A.M. A13064.

	<i>Specimen A</i>	<i>Specimen B</i>
remains of cephalothorax	47,0 mm	—
length of neck . .	23,0 mm	22,0 mm
length of trunk . .	15,0 mm	25,0 mm

Remarks

Of the seven species of *Lophoura* mentioned and figured by Yamaguti (1963) the cephalothorax is never more than 10 times longer than wide. In this character the present material differs markedly, having the cephalothorax at least 30 times longer than wide. In the structure of the knobbed process situated at the distal end of the 'neck', the present material resembles *L. tripartita* and, to a lesser extent, *L. edwardsi* in some of the variations figured by Nunés-Ruivo (1954: fig. 5). The knobbed process of *L. tripartita* is spikier and more branched than the present material (Wilson 1935: fig. 75). *L. magna* (Szidat 1971) possesses a relatively short cephalothorax, although the neck and trunk resemble *L. elongata*. *L. laticervix* (Hewitt 1964) has a short, stout neck, while the knobbed process at the base of the cephalothorax resembles the present material to some extent.

SUMMARY

A systematic account of South African parasitic Copepoda is given which supplements and revises earlier work. A catalogue of all the species of parasitic Copepoda in the South African Museum is provided. Full descriptions and figures are given of species new to science and descriptions are also given of species newly recorded from South Africa. The following new species are described: *Gunenotophorus blaisei*, *Caligus penrithi*, *Lepeophtheirus lalandei*, *Lepeophtheirus natalensis*, *Lernanthropodes natalensis*, *Lernanthropus ecclesi*, *Lernanthropus sarbae*, *Pseudocynoides rugosa*, *Lernaeniscus gonostomae*, *Brachiella lithognathae*, *Naobranchia pritchardae* and *Lophoura elongata*.

ACKNOWLEDGEMENTS

We thank the many collectors of specimens who made the present work possible. We are particularly grateful to Dr Mary-Lou Hanson Pritchard who collected most of the material described here. We are grateful to Dr P. A. Hulley for checking the names of host fishes in this paper. We thank the South African Council for Scientific and Industrial Research for grants to the second author enabling the employment of Mr Leiserowitz who prepared preliminary drawings of the material.

Species	Material	Locality	Host	Cat. No.	Type Material
Subclass COPEPODA					
Order HARPACTACOIDA					
<i>Balanophyllus unisetus</i> Aurivillius					
Order CYCLOPOIDA					
Suborder POECILOSTOMA					
Family Chondracanthidae					
<i>Acanthochondria lepidionis</i> Barnard	numerous	Durban	Sei Whale	A11058	
<i>Chondracanthus barnardi</i> Ho	1 ovig. ♀, 1 ♂ 6 ♀♀	Off Cape Point Off Cape Point	<i>Lepidion capense</i> <i>Lepidion capense</i>	A13025 A8522	Holotype & allotype Paratypes
<i>Chondracanthus colligens</i> Barnard	5 ovig. + 4 ♀♀ sev. ovig. ♀♀	Agulhas Bank Table Bay	<i>Lophius piscatorius</i> <i>Lophius piscatorius</i>	A7607 A13009	Syntypes Syntypes
<i>Chondracanthus merlucci</i> (Holten)	3 ovig. ♀♀ 8 ♂♂	Off west coast	<i>Gonypterus capensis</i>	A12591	Syntypes
<i>Chondracanthus neali</i> Leigh-Sharpe	sev. ♀♀ & ♂♂ 3 ovig. ♀♀, 3 ♂♂	Table Bay 61 km WSW Danger Point	<i>Merluccius capensis</i> <i>Merluccius</i> sp.	A1592 A13005	
<i>Chondracanthus tuberculatus</i> Nordman	4 ovig. ♀♀, 3 ♂♂ 1 ovig. ♀, 1 ♂	Table Bay Table Bay	<i>Merluccius</i> sp. <i>Merluccius</i> sp.	A13006 A11790	
<i>Cucumaria notabilis</i> Paterson	1 ovig. ♀ 15 ovig. + 4 ♀♀ 2 ovig. ♀♀, 3 ♂♂	Table Bay Off west coast 32° 15'S, 16° 30'E	<i>Malacocephalus laevis</i> <i>Malacocephalus laevis</i> <i>Malacocephalus laevis</i>	A13007 A13008 A13045	
<i>Lernentoma triglae</i> de Blainville	1 ovig. ♀, 1 ♂ 3 ovig. + 2 ♀♀, 2 ♂♂ 1 ♀, 1 ♂ 1 ♀, 3 ♂♂	Table Bay Blouberg Blouberg	<i>Congipodus torus</i> <i>Congipodus torus</i> <i>Cucumaria frauenfeldi</i>	A7612 A7612 A13037	Holotype & allotype Paratypes
<i>Medesicaste penetrans</i> Heller	1 ovig. ♀ 2 ovig. ♀♀ 1 ♀	Table Bay Table Bay Table Bay	<i>Cucumaria frauenfeldi</i> <i>Trigla capensis</i> <i>Trigla capensis</i>	A13038 A13022 A13023	
<i>Strabax monstrosus</i> Nordman	1 ovig. ♀, 1 ♂ 1 ovig. ♀ 1 ♀ 1 ovig. ♀, 1 ♂ 1 ovig. ♀ 1 ♀ 1 ovig. ♀, 1 ♂	False Bay Table Bay Table Bay Port St. Johns	<i>Trigla capensis</i> <i>Trigla capensis</i> <i>Trigla capensis</i> <i>Trigla capensis</i> <i>Trigla capensis</i> <i>Trigla capensis</i> <i>Scorpaenodes guamensis</i>	A13047 A1596 A13024 A13046 A7608	

Species	Material	Locality	Host	Cat. No.	Type Material
Suborder SIPHONOSTOMA					
Family Cancerillidae					
<i>Cancerilla tubulata</i> Dalyell	1 ovig. ♀	Lüderitzbucht	<i>Amphipholis squamata</i>	A12713	
Family Clausidae					
<i>Entobius euelpis</i> Barnard	1 ovig. ♀	?	Polychaete	A5977	Holotype
Order NOTODELPHYOIDA					
Family Notodelphyidae					
<i>Dorytpygus pulex</i> Thorell	2♀♀ 1♀ 1♀ 8♀♀ 3♀♀	St. James Port Elizabeth St. James St. James St. James	<i>Pyura stolonifera</i> Ascidian <i>Pyura stolonifera</i> <i>Pyura stolonifera</i> <i>Pyura stolonifera</i>	A2096 A13039 A1578 A1579 A2097	
<i>Gunenotophorus globularis</i> Costa	1 ovig. ♀ 1 ovig. ♀ 4 ovig. ♀♀ 2 ovig. ♀♀, 2♂♂	Cape St. Blaize Cape St. Blaize Still Bay, Cape Port Elizabeth	<i>Gynandrocarpa unilaterialis</i> <i>Gynandrocarpa unilaterialis</i> Ascidian Ascidian	A13049 A13041 A7604 A13040	Holotype Paratype
* <i>Gunenotophorus blaizei</i> n. sp.					
<i>Notodelphys allmani</i> Thorell					
Order CALIGOIDA					
Family Caligidae					
* <i>Caligus aescopus</i> Wilson	10 ovig. + 25♀♀, 4♂♂ 1 ovig. + 1♀, 1♂ 3♀♀	False Bay Durban	<i>Seriola lalandi</i> <i>Pomatomus saltator</i>	A12994 A12996	
<i>Caligus arii</i> Bassett-Smith	1 ovig. + 2♀♀ 6 ovig. ♀♀ ovig. ♀, 3♂♂	Chinde, P. E. A. Durban Cape Town	<i>Arius acutirostris</i> <i>Caranx djedabae</i> <i>Thunnus obesus</i>	A8518 A12995 A11808	
* <i>Caligus coryphaenae</i> Steenstrup & Lütken	1 ovig. ♀ 1 ovig. ♀, 1♂ 1 ovig. + 3♀♀, 1♂ 1 ovig. ♀	Algoa Bay Table Bay Kalk Bay Rocky Pt, S.W.A.	<i>Eulhymnus belamisi</i> <i>Anchoviella holodon</i> <i>Pachymetopon blochii</i> <i>Seriola lalandi</i>	A11753 A8520 A11780 A8517	Holotype Syntypes Syntypes
<i>Caligus engraulidis</i> Barnard	1♀ 1 ovig. ♀	Torra Bay, S.W.A. Möwe Bay, S.W.A.	? ?	A12709 A12991	Holotype Paratype
<i>Caligus hottentotus</i> Barnard	1♀ 2 ovig. ♀♀ 1 ovig. + 2♀♀ 2 ovig. ♀♀	Möwe Bay, S.W.A. Möwe Bay, S.W.A. Swakopmund, S.W.A. Saldanha Bay	<i>Chorisochasmus dentex</i> <i>Blennius cornutus</i> <i>Clinus superciliosus</i> <i>Blennius cornutus</i> <i>Clinus superciliosus</i>	A12992 A12993 A12990 A11814	

Species	Material	Locality	Host	Cat. No.	Type Material
<i>*Caligus penrithi</i> n. sp.	4 ovig. + 1♀, 7♂♂ 1 ovig. ♀, 1♂ 2 ovig. ♀♀, 4♂♂ 2 juv. ♀♀ 1♀	Möwe Bay, S.W.A. Möwe Bay, S.W.A. Algoa Bay	<i>Chilodactylus fasciatus</i> <i>Chilodactylus fasciatus</i> <i>Amblyrhynchotes hyphselogneion</i>	A13051 A13050 A3778	Paratypes Holotype & allotype Syntypes
<i>Caligus tetrodonis</i> Barnard	7 ovig. + 6♀♀ 1♀, 1♂ 2 ovig. ♀♀, 2♂♂ 1♀ 8 ovig. + 8♀♀, 2♂♂ 1♀ + 1♂ 6♀♀	Durban West of Cape Town Table Bay Sea Point Table Bay Port Elizabeth Verna Seamount Verna Seamount Natal ? Natal Natal East London	<i>Amblyrhynchotes hyphselogneion</i> <i>Mola mola</i> <i>Mola mola</i> <i>Mola lanceolata</i> <i>Mola mola</i> <i>Mola mola</i> <i>Seriola lalandi</i> <i>Seriola lalandi</i> <i>Hyphacanthus amia</i> <i>Carcharias leucas</i> <i>Carcharias leucas</i> <i>Carcharias leucas</i> <i>Plotosus anguillaris</i>	A1604 A11812 A4789 A13168 A11761 A11760 A13052 A13053 A7619 A12989 A13054 A13055 A8519	Holotype & allotype Paratypes Syntypes Holotype Paratypes Holotype
<i>*Lepeophtheirus lalandei</i> n. sp.	4 ovig. + 8♀♀ 3 ovig. ♀♀ 1 ovig. ♀ 11 ovig. ♀♀ 1 ovig. ♀	Natal ? Natal Natal East London	<i>Hyphacanthus amia</i> <i>Carcharias leucas</i> <i>Carcharias leucas</i> <i>Carcharias leucas</i> <i>Plotosus anguillaris</i>	A12989 A13054 A13055 A8519	Holotype & allotype Paratypes Syntypes Holotype Paratypes Holotype
<i>Lepeophtheirus lichiae</i> Barnard	7 ovig. + 9♀♀, 10♂♂ 8♀♀, 8♂♂ 1♀, 1♂ 7♀♀ 5♀♀ 2♀♀	Bantry Bay, Cape Sea Point, Cape Cape Cape Table Bay Table Bay Table Bay Table Bay Table Bay Port Elizabeth Cape Columbine Table Bay Sea Point	<i>Mola lanceolata</i> <i>Mola lanceolata</i> <i>Mola mola</i> <i>Mola mola</i> <i>Mola mola</i> <i>Mola mola</i> <i>Mola mola</i> <i>Mola mola</i> <i>Mola mola</i> <i>Mola mola</i> <i>Mola mola</i> <i>Mola mola</i> <i>Mola lanceolata</i>	A11810 A13166 A1580 A1581 A11757 A11754 A11768 A1585 A1584 A1582 A11767 A12986 A7603 A13167	Paratypes Holotype & allotype Syntypes Holotype Paratypes Holotype
<i>*Lepeophtheirus longispinosus</i> Wilson	sev. ♀♀ & ♂♂ sev. ♀♀ & ♂♂ sev. ♀♀ & ♂♂ sev. ♀♀ & ♂♂ sev. ♀♀ & ♂♂ 1♀ 3♀♀ 5 ovig. + 2♀♀	sev. ♀♀ & ♂♂ sev. ♀♀ & ♂♂ sev. ♀♀ & ♂♂ sev. ♀♀ & ♂♂ sev. ♀♀ & ♂♂ 1♀ 3♀♀ 5 ovig. + 2♀♀	<i>Lepeophtheirus longispinosus</i> Wilson		
<i>*Lepeophtheirus natalensis</i> n. sp.					
<i>Lepeophtheirus plotosi</i> Barnard					
Family Cecropidae					
<i>*Cecrops exiguus</i> Wilson					
<i>Cecrops latreillei</i> Leach					
<i>Orthogoriscicola muricatus</i> (Krøyer)					
<i>Philothagoriscus serratus</i> (Krøyer)					

Species	Material	Locality	Host	Cat. No.	Type Material
Family Euryphoridae					
<i>Alebian carcharias</i> (Krøyer)					
	1 ovig. ♀	West of Slangkop	<i>Carcharodon carcharias</i>	A11770	
	2♀♀	Off Cape Point	<i>Carcharhinus obscurus</i>	A11769	
	3 ovig. + 4♀♀	Durban.	<i>Odontaspis</i> sp.	A12972	
	1♀	Ifafa, Natal	Shark	A12973	
*Elytrophora hemiptera Wilson					
	5♀♀, 8♂♂	West of Cape Point	<i>Thunnus thynnus</i>	A11809	
	1 ovig. + 1♀	Table Bay	<i>Thunnus albacora</i>	A11793	
Gloiopotes watsoni Kirtisinghe					
	4 ovig. ♀♀, 2♂♂	Mossel Bay	<i>Makaira audax</i>	A11795	
	4♀♀, 3♂♂	Mossel Bay	<i>Makaira indica</i>	A11796	
	sev. ♀♀ & ♂♂	S.W. of Cape Point	<i>Makaira audax</i>	A11756	
	sev. ♀♀ & ♂♂	S.W. of Cape Point	<i>Makaira audax</i>	A11758	
	sev. ♀♀ & ♂♂	Off Cape Point	<i>Makaira indica</i>	A12975	
	sev. ♀♀ & ♂♂	Off Slangkop	<i>Makaira indica</i>	A11799	
	sev. ♀♀ & ♂♂	Off Slangkop	<i>Makaira audax</i>	A11797	
	4 ovig. ♀♀, 4♂♂	Off Cape Point	<i>Makaira audax</i>	A13172	
	sev. ♀♀ & ♂♂	Off Cape Point	<i>Makaira indica</i>	A11798	
Family Pandaridae					
<i>Achtheinus dentatus</i> Wilson					
	3 ♀♀	Buffels Bay, Cape	?	A1588	
	4 ♀♀, 1♂	False Bay	<i>Mustelus</i> sp.	A7618	
	sev. ♀♀ & ♂♂	33° 55'S, 25° 46'E	Shark	A1587	
	sev. ♀♀ & ♂♂	Algoa Bay	Shark	A4245	
	sev. ♀♀ & ♂♂	Table Bay	<i>Carcharodon carcharias</i>	1365	
	1♀	West coast	<i>Squalus blainvilliei</i>	A12978	
	sev. ♀♀ & ♂♂	False Bay	<i>Mustelus canis</i>	A12979	
	sev. ♀♀ & ♂♂	Strand, Cape	<i>Sphyrna zygaena</i>	A12980	
	sev. ♀♀ & ♂♂	Orange River mouth	<i>Haploblepharus edwardsi</i>	A12981	
	sev. ♀♀ & ♂♂	False Bay	<i>Squalus acanthias</i>	A12982	
	sev. ♀♀ & ♂♂	Langebaan, Cape	<i>Mustelus canis</i>	A12983	
	sev. ♀♀ & ♂♂	Table Bay	<i>Haploblepharus edwardsi</i>	A12984	
	sev. ♀♀ & ♂♂	Table Bay	<i>Pliotrema warreni</i>	1366	
Achtheinus dentatus Wilson					
	4 ♀♀	?	<i>Prionace glauca</i>	A11781	
	3 ovig. ♀♀	S.W. of Cape Town	<i>Mola mola</i>	A12836	
	4 ♀♀	West of Cape Point	<i>Isurus glaucus</i>	A8532	
	1♀	?	<i>Isurus</i> sp.	A12974	
	4 ♀♀	Off Cape Point	<i>Isurus glaucus</i>	A11766	
	sev. ♀♀ & ♂♂	Off Cape Point	?	A11804	
Family Achtheinidae					
<i>Achtheinus cf. pinguis</i> Wilson					
Dinematura latifolia Steenstrup & Lütken					

Species	Material	Locality	Host	Cat. No.	Type Material
<i>Echthrogaleus coleoptratus</i> (Guérin)	1 ovig. ♀ 1 ♀	False Bay	<i>Prionace glauca</i>	A8523	
* <i>Echthrogaleus torpedinis</i> Wilson	1 ovig. ♀ 3 ovig. ♀♀ sev. ovig. ♀♀ sev. ♀♀ & ♂♂ sev. ovig. ♀♀ 2 ovig. + 1 ♀♀ 3 ovig. + 1 ♀♀ 7 ♂♂	Off Slangkop Off Cape Columbine West of Slangkop Durban ? False Bay Durban Three Anchor Bay	<i>Prionace glauca</i> <i>Torpedo nobiliana</i> <i>Torpedo</i> sp. <i>Carcharodon carcharias</i> <i>Sphyrna zygaena</i> <i>Carcharodon carcharias</i> <i>Carcharinus</i> sp. ?	A12987 A12988 A12215 A12969 A12970 A13171 A11786 A1601	
<i>Pandarus bicolor</i> Leach	11 ovig. + 3 ♀♀, 5 ♂♂ 6 ovig. + 1 ♀♀ 9 ovig. + 2 ♀♀ 10 ovig. + 1 ♀♀ 14 ovig. + 9 ♀♀ 1 ♀ 6 ovig. + 5 ♀♀ 5 ovig. + 2 ♀♀ 2 ♀♀	Table Bay False Bay Sea Point Natal Durban Natal Milnerton Off Slangkop West of Slangkop Off Slangkop Durban ? Off Cape Point Table Bay ?	<i>Odontaspis</i> sp. <i>Galeorhinus galeus</i> Dogfish <i>Sphyrna zygaena</i> <i>Stegostoma</i> sp. ? <i>Rhincodon typus</i> <i>Rhincodon typus</i> <i>Prionace glauca</i> <i>Carcharodon carcharias</i> <i>Isurus oxyrinchus</i> <i>Odontaspis</i> sp. <i>Isurus</i> sp. <i>Carcharinus obscurus</i> <i>Odontaspis</i> sp. <i>Scoliodon palasorrah</i> <i>Scoliodon</i> sp.	A3104 A7614 A2995 A7616 A7615 A1591 A12997 A12998 A12999 A11764 A13000 A11785 A11762 A11763 13536 A7617 A12971	
<i>Pandarus smithi</i> Rathbun	1 ovig. ♀ 3 ovig. ♀♀	Off Cape Point Table Bay Durban	<i>Isurus</i> sp.		
<i>Perissopus dentatus</i> Steenstrup & Lütken	13 ♀♀ 1 ♀	Table Bay 34° 23' S, 18° 40' E	Skate Skate	A1589 A11752	
Family Trebiidae <i>Trebius caudatus</i> Krøyer	sev. ♀♀ & ♂♂ sev. ♀♀ & ♂♂ sev. ♀♀ & ♂♂ sev. ♀♀ & ♂♂ sev. ♀♀ & ♂♂	Table Bay ? Durban Off Cape Point Off Slangkop	<i>Odontaspis</i> sp. <i>Isurus</i> sp. <i>Isurus</i> sp. <i>Isurus</i> sp. <i>Isurus oxyrinchus</i>	A7605 A11759 A12976 A11801 A12977	
Family Anthosomatidae <i>Anthosoma crassum</i> (Abildgaard)					

Species	Material	Locality	Host	Cat. No.	Type Material
* <i>Lernanthropodes natalensis</i> n. sp. * <i>Lernanthropus corniger</i> Yamaguti	sev. ♀♀ & ♂♂	West of Cape Point	<i>Isurus glaucus</i>	A8531	
	sev. ♀♀ & ♂♂	Durban	<i>Carcharodon carcharias</i>	A11787	
	sev. ♀♀ & ♂♂	False Bay	<i>Carcharodon carcharias</i>	A13169	
	1 ovig. ♀	Durban	<i>Chorinemus tol</i>	A13034	Holotype
* <i>Lernanthropus ecclesi</i> n. sp. * <i>Lernanthropus sarbae</i> n. sp.	3 ovig. + 5 ♀♀	Durban	<i>Caranx djedaba</i>	A13016	
	2 ovig. ♀♀	Durban	<i>Caranx djedaba</i>	A13017	
	5 ovig. ♀♀	Durban	<i>Caranx djedaba</i>	A13018	
	1 ovig. ♀, 1 ♂	Durban	<i>Caranx djedaba</i>	A13019	
Family Dichelesthiidae <i>Hatschekia acuta</i> Barnard	8 ovig. + 2 ♀♀, 6 ♂♂	False Bay	<i>Seriola lalandi</i>	A13021	Holotype & allotype
	1 ovig. ♀, 1 ♂	False Bay	<i>Seriola lalandi</i>	A13057	Paratypes
	1 ♀	Durban	<i>Rhabdosargus sarba</i>	A13056	Holotype & allotype
		Durban	<i>Rhabdosargus sarba</i>	A13056	Paratype
Family Eudactylinidae * <i>Kroyeria carchariae</i> Hesse * <i>Nemesis lamna</i> Risso <i>Nemesis pallida</i> Wilson	15 ♀♀	Fish Hoek, Cape	<i>Brama raii</i>	A8521	Syntypes
	12 ♀♀	Off west coast	<i>Brama raii</i>	A13004	
	2 ♀♀	32° 15' S, 16° 30' E	<i>Brama raii</i>	A13044	
	26 ovig. + 13 ♀♀	Fish Hoek, Cape	<i>Prionace glauca</i>	A13001	
Family Pseudocynidae * <i>Pseudocynoides rugosa</i> n. sp.	sev. ovig. ♀♀	False Bay	<i>Carcharodon carcharias</i>	A13170	
	1 ovig. ♀	Fish Hoek, Cape	<i>Prionace glauca</i>	A13002	
	sev. ♀♀ & ♂♂	Table Bay	<i>Alopias vulpes</i>	A2590	
	sev. ♀♀ & ♂♂	Off west coast	<i>Alopias vulpes</i>	A3093	
Family Lernaieidae <i>Cardiodectes medusaeus</i> (Wilson)	1 ovig. ♀	Durban	<i>Scomberomorus maculatus</i>	A13058	Holotype
	3 ovig. ♀♀	Durban	<i>Scomberomorus maculatus</i>	A13059	Paratypes
	4 ovig. ♀♀	N.E. of Cape Point	Myctophid	A1594	
	2 ovig. ♀♀	Off Cape Point	Myctophid	A1602	
* <i>Lernaeniscus gonostomae</i> n. sp. * <i>Peniculisia furcata</i> (Krøyer)	1 ovig. ♀	Off Cape Point	<i>Goniichthys coxii</i>	A1603	
	1 ovig. ♀	Off Cape Point	? <i>Scopelus</i> sp.	A1595	
	9 ovig. ♀♀	N.W. of Slangkop	Myctophids	A11813	
	1 ovig. ♀	33° 10' S, 17° 20' E	<i>Lampanyctodes hectoris</i>	A13035	
* <i>Lernaeniscus gonostomae</i> n. sp. * <i>Peniculisia furcata</i> (Krøyer)	1 ovig. ♀	West of Slangkop	<i>Lampanyctodes hectoris</i>	A13036	
	1 ovig. ♀	26° 30' S, 33° 40' E	<i>Gonostoma elongatum</i>	A11751	Holotype
	1 ovig. ♀	26° 30' S, 33° 40' E	<i>Gonostoma elongatum</i>	A13173	Paratype
	1 ♀	28° 12' S, 33° 24' E	<i>Gonostoma elongatum</i>	A13031	Paratype
* <i>Lernaeniscus gonostomae</i> n. sp. * <i>Peniculisia furcata</i> (Krøyer)	6 ovig. + 1 ♀♀	Inhaca Island	<i>Paramonacanthus barnardi</i>	A13011	

Species	Material	Locality	Host	Cat. No.	Type Material
Family Pennellidae					
Family Pennellidae					
<i>Pennella balaenopterae</i> Koren & Danielssen	1 ♀ 2 ovig. ♀♀	False Bay Saldanha Bay	<i>Balaenoptera physalus</i> Whale	A7596 A5982	
<i>Pennella crassicornis</i> Steenstrup & Lütken	3 ♀♀ 2 ovig. ♀♀	Table Bay False Bay	<i>Balaenoptera acutorostrata</i> <i>Thynnus albacores</i>	A3101 A13043	
<i>Pennella filosa</i> (Linnaeus)	3 ovig. ♀♀ 3 ovig. ♀♀	Table Bay Off Cape Point	<i>Mola mola</i> <i>Makaira indica</i>	A7595 A11788	
<i>Pennella orthogorisci</i> Wright	3 ovig. ♀♀	Off Cape Point	<i>Physeter catodon</i> , <i>Balaenoptera borealis</i> ,		
<i>Pennella</i> sp.	many ♀♀	Saldanha Bay	<i>Balaenoptera physalus</i>		
Order LERNAEOPODOIDA					
Family Lernaepodidae					
<i>Brachiella supplicans</i> Barnard	7 ovig. ♀♀, 1 ♂ 1 ♀, 2 ♂♂	Table Bay Table Bay	<i>Genypterus capensis</i> <i>Genypterus capensis</i>	A12592 A13048	Syntypes
* <i>Brachiella lithognathae</i> n. sp.	1 ovig. ♀, 1 ♂ 2 ovig. ♀♀ 2 ovig. ♀♀ 2 ovig. ♀♀ 2 ovig. ♀♀ 1 ovig. ♀, 1 ♂	Rocky Pt, S.W.A. Rocky Pt, S.W.A. Table Bay Table Bay Off west coast Off west coast	<i>Lithognathus aureti</i> <i>Lithognathus lithognathus</i> <i>Raja</i> sp. <i>Raja</i> sp. <i>Raja caudaspinosa</i> <i>Raja leopardus</i>	A13060 A11792 A13012 A13013 A13014	Holotype & allotype Paratypes Paratypes
<i>Charopinus dubius</i> Scott	1 ♀ 1 ♀	Off Cape Point Off Cape Point	<i>Etmopterus</i> sp. <i>Etmopterus</i> sp.	A12108 A13061	
* <i>Lernaepoda etmopterae</i> Yamaguti	1 ♀ 3 ovig. ♀♀ 25 ovig. ♀♀	False Bay False Bay False Bay	<i>Sardinops ocellata</i> <i>Sardinops ocellata</i> <i>Lithognathus lithognathus</i>	A13032 A13062 A7610	
* <i>Clavellisa</i> cf. <i>ilishae</i> Pillai	2 ovig. ♀♀, 1 ♂ 5 ovig. ♀♀, 2 ♂♂ 7 ovig. ♀♀ 1 ovig. ♀	Durban Durban East London Natal	<i>Chirocentrus dorab</i> <i>Lithognathus lithognathus</i> <i>Pagrus nasutus</i> <i>Sciaenops ocellatus</i>	A13033 A7610 A8525 A8527	
<i>Clavellodes pagelli</i> (Krøyer)	18 ovig. + 6 ♀♀ 14 ovig. + 2 ♀♀ 2 ovig. ♀♀ 15 ovig. ♀♀	West coast False Bay False Bay Table Bay	<i>Pachymetopon blochii</i> <i>Argyrozona argyrozona</i> <i>Chrysoblephus laticeps</i> <i>Pachymetopon blochii</i>	A13026 A13027 A13028 A13029	
* <i>Clavellopsis appendiculata</i> Kirtisinghe	8 ovig. ♀♀, 2 ♂♂	Table Bay	<i>Congioptodus torus</i>	A7611	Syntypes
<i>Clavellopsis fallax</i> (Heller)					
<i>Clavellopsis hostilis</i> (Heller)					
* <i>Clavellopsis sargi</i> (Kurz)					
<i>Eubrachiella sublobulata</i> Barnard					

Species	Material	Locality	Host	Cat. No.	Type Material
<i>Lerneopoda galei</i> Krøyer	1 ovig. ♀	False Bay	<i>Mustelus laevis</i>	A7613	
<i>Parabranchiella australis</i> Wilson	1 ovig. ♀, 1 ♂	?	<i>Merluccius capensis</i>	A8524	
	1 ovig. ♀	Table Bay	<i>Merluccius capensis</i>	A11791	
<i>Naobranchia pritchardae</i> n. sp.	1 ovig. ♀	Durban	<i>Pomadourys operculare</i>	A13042	Holotype
	1 ovig. ♀	Durban	<i>Pomadourys operculare</i>	A13063	Paratype
Family Spyriidae					
* <i>Lophoura elongata</i> n. sp.	1 ♀	Off Cape Point	<i>Synaphobranchius bathybius</i>	A11802	Holotype
	1 ♀	Off Cape Point	<i>Synaphobranchius bathybius</i>	A13064	Paratype
* <i>Schisobranchia ramosa</i> (Krøyer)	3 ovig. ♀♀	Table Bay	<i>Raja douteri</i>	A13015	
<i>Sphyryon laetigatum</i> Guérin-Meneville	1 ovig. ♀	Off Cape Point	?	A2094	
	2 ovig. ♀♀	Table Bay	<i>Genypterus capensis</i>	A7606	
	1 ♀	Off Cape Point	<i>Macrurus</i> sp.	A3105	
	1 ♀	Table Bay	?	A1593	
	1 ovig. ♀	Off Cape Point	<i>Coelorhynchus fasciatus</i>	A2093	
	1 ♀	West of Cape Point	<i>Genypterus capensis</i>	A11807	
	1 ♀	West of Cape Town	<i>Genypterus capensis</i>	A12107	
	5 ♀♀	West of Slangkop	<i>Genypterus capensis</i>	A12570	
	1 ovig. ♀	Off Cape Town	<i>Genypterus capensis</i>	A12213	
	1 ♀	Off Cape Point	<i>Antimora</i> sp.	A13003	
	8 ♀♀	Off Cape Point	<i>Cottunculus</i> sp.	A4242	
		St. Helena Bay	From seal stomach	A1598	
				A8530	
Subclass Branchiura					
Order ARGULOIDA					
Family Argulidae					
<i>Argulus belones</i> van Kamper	4 ♀♀	Natal	<i>Scomberomorus commersoni</i>	A8529	
<i>Argulus multipocula</i> Barnard	1 ovig. ♀	Richards Bay, Natal	?	A13065	Holotype
<i>Chonopeltis inermis</i> Thiele	3 juv.	Okavango, S.W.A.	<i>Synodontis melanostictus</i>	A8528	
<i>Dolops ranarum</i> (Stuhlmann)	3 ♀♀, 6 ♂♂	Hartebeespoort Dam, Transvaal	<i>Tilapia mossambica</i>	A11776	
		Matopla Dam, Bulawayo	<i>Haro salmonoides</i>	A11777	

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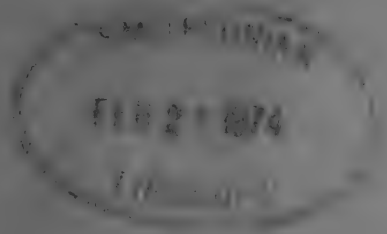
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ANACANTHOBATIS MARMORATUS
VON BONDE & SWART, 1923

By
P. A. HULLEY

Cape Town Kaapstad

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By

P. A. HULLEY

South African Museum, Cape Town

(With 14 figures and 2 tables)

[MS. accepted 5 March 1973]

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INTRODUCTION

In 1923 Von Bonde & Swart described two new species of skate, *Anacanthobatis marmoratus* and *A. dubius*, from off the coast of Natal, South Africa (the proposed name *Leiobatis* being preoccupied—Errata Slip, Von Bonde & Swart 1923). The species were included in a separate family Anacanthobatidae, which was considered to be part of the Masticura (=Myliobatoidea). Because of this suggested relationship and because of the structure of the teeth and lack of dorsal fins, Barnard (1925), Fowler (1941) and Smith (1961) included the genus in the family Dasyatidae. However, Bigelow & Schroeder (1951, 1953, 1962) and Hulley (1972a) consider that the nature of the pelvic fins, the presence of lateral prepelvic processes on the pelvic girdle and the number of proximal basal segments in the clasper preclude their incorporation with the Dasyatidae, and recognize the Anacanthobatidae as a distinct family of the order Rajoidea. This distinction is supported by the typical rajoid egg case in *Anacanthobatis marmoratus* (Wallace 1967).

At present, two genera are recognized within the family, *Anacanthobatis*

(*A. marmoratus*, *A. longirostris*, *A. americanus*, *A. borneensis*) and *Springeria* (*S. foliorostris*, *S. melanosoma*, *S. ori*), and *A. dubius* is now considered to be a junior synonym of *A. marmoratus* (Bigelow & Schroeder 1962; Wallace 1967). Many of the initial definitive characters for the genus *Springeria* (Bigelow & Schroeder 1951) have fallen away with further taxonomic investigation (Bigelow & Schroeder 1953, 1962; Chan 1965a; Wallace 1967), so that the recognition of the genus now rests solely on the terminal leaf-like expansion of the snout.

During the course of investigations on the interrelationships of southern African Rajidae (Hulley 1972a), the claspers of *Anacanthobatis marmoratus* and *A. americanus* were briefly examined by the author. Basic major differences in the clasper structure suggested that two genera were possibly involved and that the family Anacanthobatidae, as defined at present, might be diphyletic and have a comparatively early origin (Hulley 1972a: fig. 57). However, these conclusions were only tentatively advanced until an investigation could be extended to other anacanthobatid species. This paper represents the results of such an investigation.

MATERIAL AND METHODS

Type specimens of the following species were examined: *Anacanthobatis marmoratus* (RUSI 662), *A. borneensis* (BMNH 1965. 1. 29. 1), *A. longirostris* (USNM 196446), *Springeria melanosoma* (USNM 198121) and *S. ori* (ORI B 187, B 188); and specimens of *A. marmoratus* (ORI B 2, B 3, B 174, B 202), *A. longirostris* (ORE 10827), *A. americanus* (ORE 10602/SAM 26626) and *S. foliorostris* (ORE 10440, 10898) were also examined. X-ray photographs of the type specimen of *Springeria foliorostris* (USNM 152546) were supplied by the United States National Museum.

BMNH=British Museum (Natural History); ORE='Oregon II' Station (material at USNM); ORI=Oceanographic Research Institute, Durban; RUSI=J. L. B. Smith Institute of Ichthyology, Grahamstown; SAM=South African Museum; USNM=United States National Museum.

The structure of the claspers appears to be the most reliable basis on which to interpret interrelationships within the Rajoidea (Ishiyama 1958; Stehmann 1970; Hulley 1970, 1972a), so that this method has been employed in the present study. However, *Springeria melanosoma* and *S. ori* are known only from juvenile females, so that additional criteria have been used.

DESIGNATION AND DESCRIPTION OF THE LECTOTYPE OF *ANACANTHOBATIS MARMORATUS*

The type-species *Anacanthobatis marmoratus* Von Bonde & Swart, 1923 was based on two syntypes, a female (245 mm total length) and a male (238 mm total length) both trawled at 30°09, 45'S, 30°58, 02'E in 292.5 m. These specimens were housed in the collection of the Government Marine Survey,

Cape Town. Unfortunately, this collection was later broken up and a large proportion of it was lost to posterity. However, during the preparation of his book *Sea fishes of southern Africa*, a number of specimens from this collection was donated to the late Professor J. L. B. Smith, among which was a single male specimen of *Anacanthobatis marmoratus*. Smith was informed that this specimen was the 'type' (M. M. Smith, personal communication), and it was photographed for inclusion in the book (Smith 1961: fig. 84). The female specimen is missing.

I now designate this male specimen (RUSI 662), housed in the collection of the J. L. B. Smith Institute of Ichthyology, Grahamstown, as the lectotype of the species *Anacanthobatis marmoratus* Von Bonde & Swart, 1923.

Anacanthobatis marmoratus Von Bonde & Swart, 1920

(Fig. 1A, B)

Lectotype

A male (232.9 mm total length), trawled at 30°09, 45'S, 30°58, 02'E in 292.5 m by the S.S. *Pickle* (Station 152); in the collection of the J. L. B. Smith Institute of Ichthyology (RUSI 662).

Description

Disc from base of rostral filament about 1.2 times as broad as long, its width 1.5 in total length excluding filament; maximum angle from base of filament to level of spiracles about 102°; end of snout with rostral filament arising from small, bluntly-rounded protuberance; anterior margins of disc concave behind level of protuberance and again at level of spiracles; outer angles rounded; posterior margins evenly convex. Axis of greatest breadth 1.1 times as far from base of filament as from posterior edge of disc. Tail slender, about 2.0 in total length from base of filament, with narrow lateral folds extending to its base.

Skin perfectly naked everywhere and without dermal denticles of any sort, but with 2 rows of hooked alar spines at outer angles of disc.

Snout in front of orbits 3.8 times as long to base of filament as distance between orbits; its length in front of mouth 3.9 times as great as distance between nostrils. Eye 1.7 times as long as spiracles; distance between orbits 1.1 times as great as length of orbit. Rostral cartilage extending to base of rostral filament as hard bar, without a segment; tip of rostral bar forming bluntly-rounded protuberance at base of filament. Anterior rays of pectorals extending almost to rostral appendices.

Mouth slightly arched; nasal curtain fringed; expanded posterior margin of nostril fringed, and overlapping corners of mouth. Teeth arranged in 29 regular rows in upper jaw, with large round bases and laterally directed, sharp, posterior cusps.



Fig. 1. *Anacanthobatis marmoratus* Von Bonde & Swart. LECTOTYPE (RUSI 662). A. dorsal view; B. ventral view.

TABLE I

Anacanthobatis marmoratus. (Lectotype.) Measurements expressed in millimetres and as percentage of the total length to base of filament. Figures in parentheses refer to Von Bonde & Swart (1923).

	mm	%
Total length	232,9 (238)	—
Total length to base of filament	230,4	100,0
Length of filament	2,5	1,1
Disc width	152,3 (155)	66,1
Disc length	130,7	56,7
Snout to greatest disc width	69,5	30,2
Snout to axils of pelvics	94,5	41,0
Snout length: in front of orbits	31,1	13,5
in front of mouth	31,5	13,6
in front of nostrils	26,6	11,5
Eye: horizontal diameter	7,4	3,2
distance between eyes	8,1	3,5
Spiracle: length	4,5	1,9
distance between spiracles	19,6	8,5
Mouth: width	15,4	6,7
Nostrils: distance between inner ends	14,6	6,3
Gill slits: length 1st	2,1	0,9
3rd	2,6	1,1
5th	2,0	0,9
distance between 1st	28,6	12,4
5th	15,8	6,9
Pelvics: length anterior margin	36,0	15,6
length posterior margin	32,4	14,1
base width	8,2	3,6
Caudal fin: upper base length	17,2	7,4
lower base length	9,6	4,1
Snout to middle of vent	111,2	48,3
Middle of vent to tip of tail	119,2 (123)	51,7

Pelvics divided into slender, limb-like, anterior lobe, arising separately from ventral surface of disc, and posterior, fin-like lobe. Posterior lobe free from inner pectoral margin, but posterior margin joined to tail almost to tip of fin.

Dorsal fins absent. Caudal fin membranous, with epiural lobe larger than hypural lobe.

Colour (in alcohol): dorsal surface irregularly mottled light brown and white, with scattered ocelli; papillae and rostral filament dark brown. Ventral surface uniformly pale.

PELVIC GIRDLE

The pelvic girdles of *Anacanthobatis marmoratus* and *A. americanus* have been described by Hulley (1972a).

In all Rajoidea, the pelvic girdle consists of a simple transverse bar, which is expanded at the iliac regions and possesses a pair of anteriorly-directed, lateral prepelvic processes. Paired iliac processes arise posteriorly from the iliac region, but recurve dorsally to terminate as blunt processes.

The pelvic girdle in the Anacanthobatidae (Fig. 2) is typically U-shaped

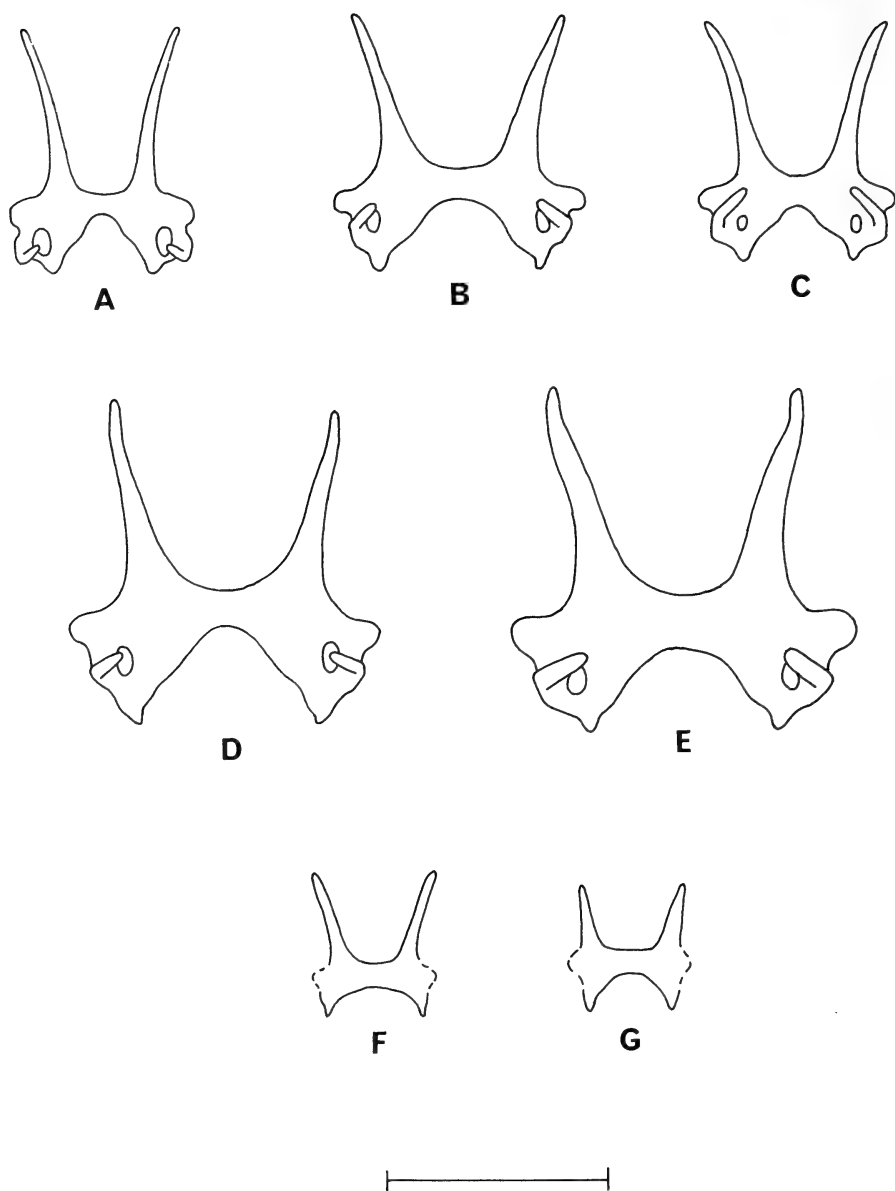


Fig. 2. Pelvic girdles of the Anacanthobatidae. A. *Anacanthobatis marmoratus* (♂); B. *A. borneensis* (♂); C. *A. americanus* (♂); D. *A. longirostris* (♂); E. *Springeria foliorostris* (♂); F. *S. ori* (♀); G. *S. melanosoma* (♀). Scale 20 mm.

with the iliac regions considerably more developed than in the Rajidae, and possesses elongate prepelvic processes. These appear to serve only for the attachment of the abdominal musculature and have no relationship to the musculature of the anterior, limb-like lobe of the pelvic fin. The three groups of muscles which are responsible for dorso-ventral movement of the anterior lobe (ventral muscles of the marginal ray—Frechkop 1925) insert at the bases of the prepelvic processes. The comparative lengths of the prepelvic processes vary considerably: *Anacanthobatis marmoratus* (0,6–0,8 times the girdle width); *A. longirostris* (0,6–0,7); *A. americanus* (0,8); *A. borneensis* (0,6); *Springeria foliorostris* (0,6–0,8); *S. ori* (0,8); and *S. melanosoma* (0,5). In all species, the processes project laterally, except in *Anacanthobatis longirostris* and *Springeria foliorostris* (Fig. 2), in which the distal extremities recurve medially.

There is a single, large obturatorial foramen on each side in all species. Sexual dimorphism is exhibited by the girdle, so that the girdle in females has a comparatively longer ischio-pubic bar. This is probably associated with the oviparous behaviour of the family.

ROSTRAL FILAMENT AND TERMINAL EXPANSION

The rostral filament and terminal expansion of the snout of all described anacanthobatid species are illustrated in Figure 3. The rostral filament, which varies in length intraspecifically, arises from a small, bluntly-rounded protuberance at the anterior extremity of the snout. This protuberance is found in all species and should not be confused with the terminal leaf-like expansion of the snout in *Springeria foliorostris* (Fig. 3E). In this species, the anterior margins of the disc are markedly constricted against the rostral bar some little distance behind the protuberance, so as to encompass the rostral appendices, i.e. the appendices themselves form the expansion. This is not found in either *Springeria ori* or *S. melanosoma* (Figs 3F, G). In these species, only a blunt anterior protuberance is present. This is formed by the anterior extremity of the rostral bar in relation to the leading edges of the rostral appendices, and has its counterpart in all other species of the genus *Anacanthobatis* (Fig. 3).

PECTORAL AND PELVIC FIN RADIALS

Quignard (1965) and Stehmann (1970) have discussed the distribution of pectoral fin radials in the Rajidae and the taxonomic value of the total number of radials in each wing. It appears that while the distribution of pectoral radials may vary intraspecifically and may even vary on opposite sides of the same individual, the total count may, in some cases be used to distinguish between closely related species, e.g. *Raja oxyrinchus* and *R. nidarosiensis*. Furthermore, it appears that this criterion may even be valid at the subgeneric level in certain instances, e.g. *Raja alba* (Stehmann 1970: fig. 13). However, Stehmann (1970) points out that in general natural combinations

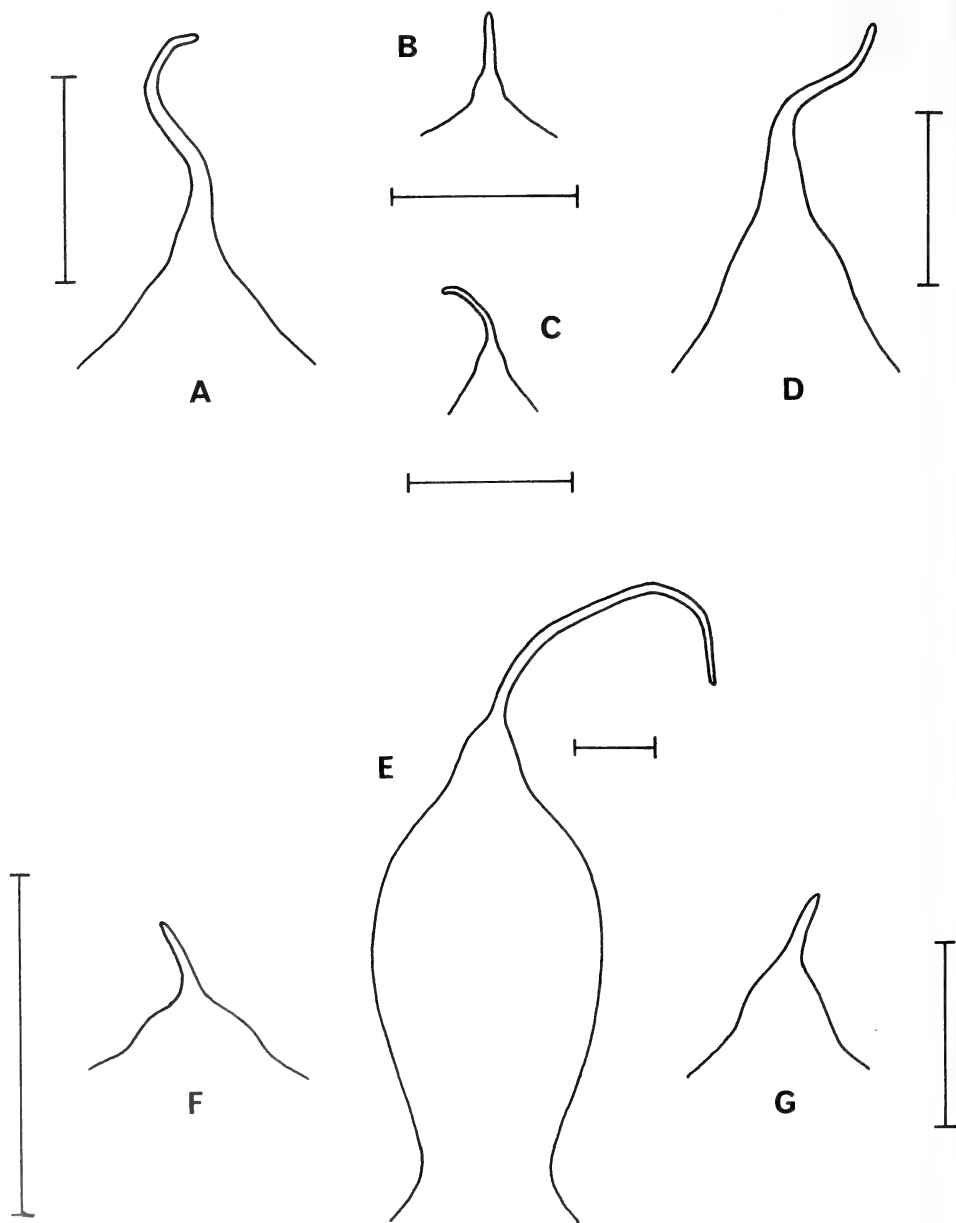


Fig. 3. Rostral filament and terminal expansion of the Anacanthobatidae. A. *Anacanthobatis marmoratus*; B. *A. americanus*; C. *A. borneensis*; D. *A. longirostris*; E. *Springeria foliorostris*; F. *S. melanosoma*; G. *S. ori.* Scale 5 mm.

of species cannot be recognized by mean values of the count.

To assess the value of this method in the Anacanthobatidae, pectoral and pelvic fin radial counts were made from X-ray photographs. The results are presented in Table 2. Since there is no overlap of the pectoral and pelvic fins, direct counts could be obtained from the plates. This method could not be applied to *Springeria melanosoma* and to certain counts in *S. ori*, due to the poor degree of calcification of the radial cartilages.

TABLE 2

Pectoral and pelvic radials in the Anacanthobatidae.

Species	No. Specimens	Total Pectoral	No. Mesopterygial	No. Intercalary	Total Pelvic
<i>A. marmoratus</i>	.. 5	72-78	3-5	11-13	13-18
<i>A. borneensis</i>	.. 1	75	4	15	14
<i>A. longirostris</i>	.. 2	88-90	4-5	16-19	14-19
<i>A. americanus</i>	.. 1	66	3	11	12
<i>S. foliorostris</i>	.. 3	87-89	6	16-18	16-19
<i>S. ori</i>	.. 1	70	—	—	13-14

CLASPER STRUCTURE

A description of the external and internal structure of the claspers of *Anacanthobatis marmoratus* and *A. americanus* has already been given (Hulley 1972a). The terminology of the various components and cartilages of the species examined in this paper are in accordance with the definitions given by Hulley (1972a). However, a further term, palp, is now defined:

palp

A fleshy pad, situated in the dorsal lobe of the clasper glans at about the level of the hypopyge, and lying along the outer lateral margin of the closed glans: with or without a distal filament; the internal support provided by the distal projection of the dorsal marginal cartilage.

It should be noted that the component usually associated with the distal projection of the dorsal marginal is the pseudorhipidion. However, the distinction between these two components has been made because the pseudorhipidion extends distally and medially in the glans as a sharp-edged cartilaginous tongue while the palp extends distally and laterally as a well-developed fleshy pad, not unlike the foot of a bivalve mollusc. Furthermore, in species in which the pseudorhipidion is present, the rhipidion is absent, the probable function of the pseudorhipidion being to spread the ejaculating spermatozoa (Leigh-Sharpe 1920). But anacanthobatids which possess a palp, also possess a rhipidion, indicating a different function for the palp and pseudorhipidion.

Springeria foliorostris (Figs 4, 5, 6)

Claspers comparatively short and naked, with slightly expanded glans more or less dorso-ventrally flattened and pointed; pseudosiphon absent; spur well developed, forming, together with palp, the outer lateral margin of dorsal

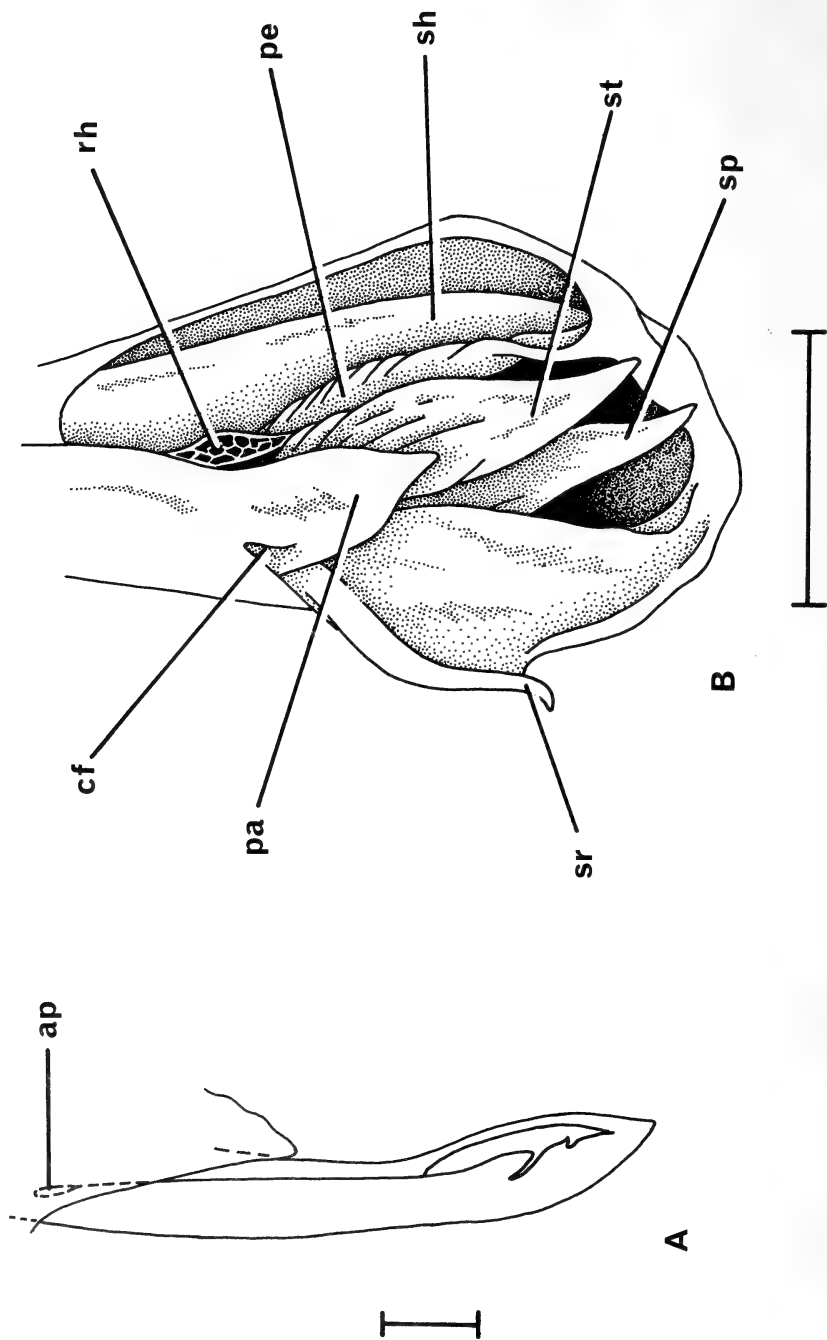


Fig. 4. *Springeria foliorostris*. A. external view of right clasper from dorsal side; B. lateral view of right clasper opened to show structural features of the glans. Scale 10 mm.
 ap—apophyle; cf—cleft; pa—palp; pe—pent; rh—rhypidium; sh—shield; sr—spur; st—sentinel.

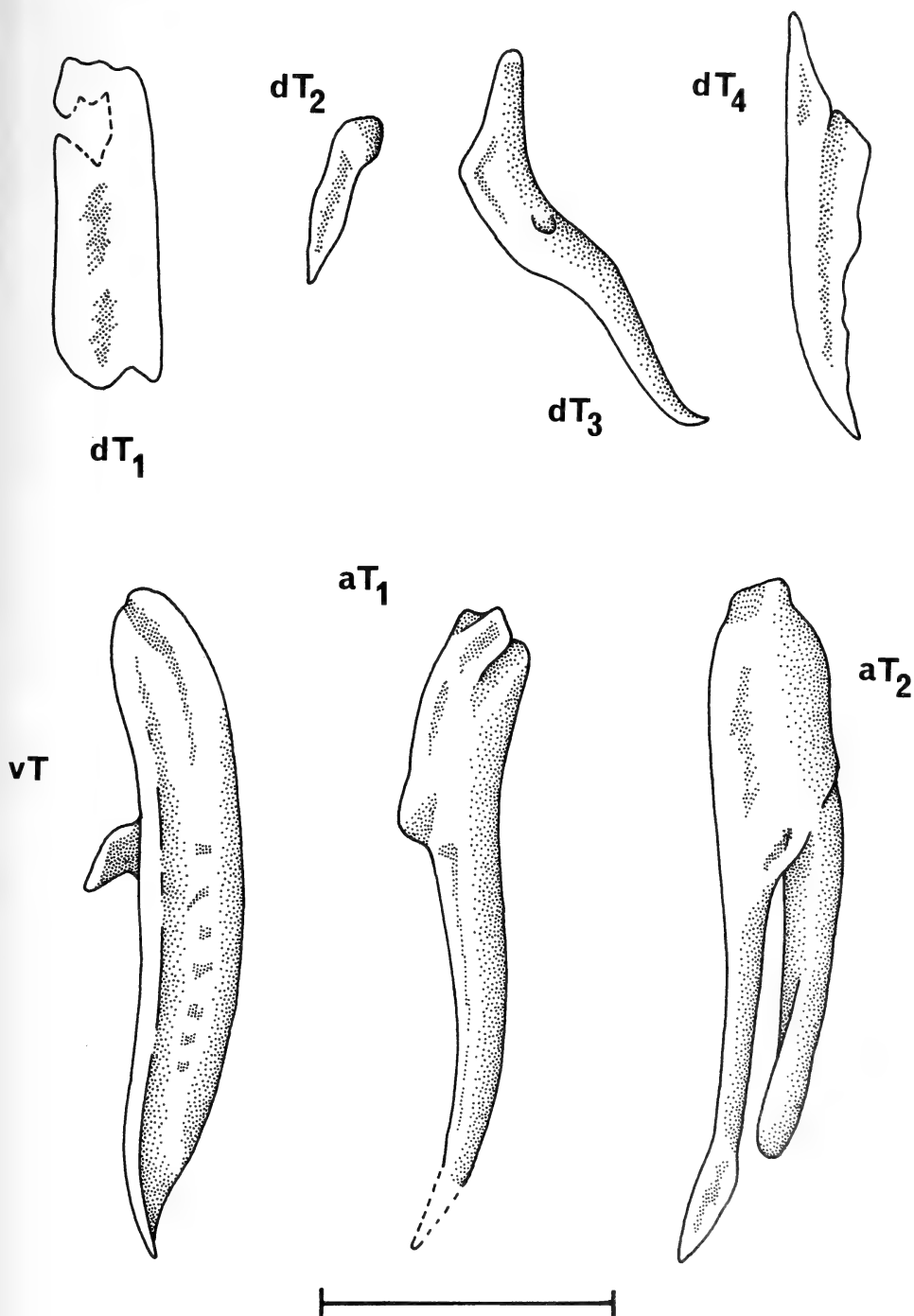


Fig. 5. *Springeria foliorostris*. Terminal cartilages of the right clasper. dT₁, dT₂, dT₃, dT₄, vT—dorsal view; aT₁, aT₂—ventral view. Scale 10 mm.

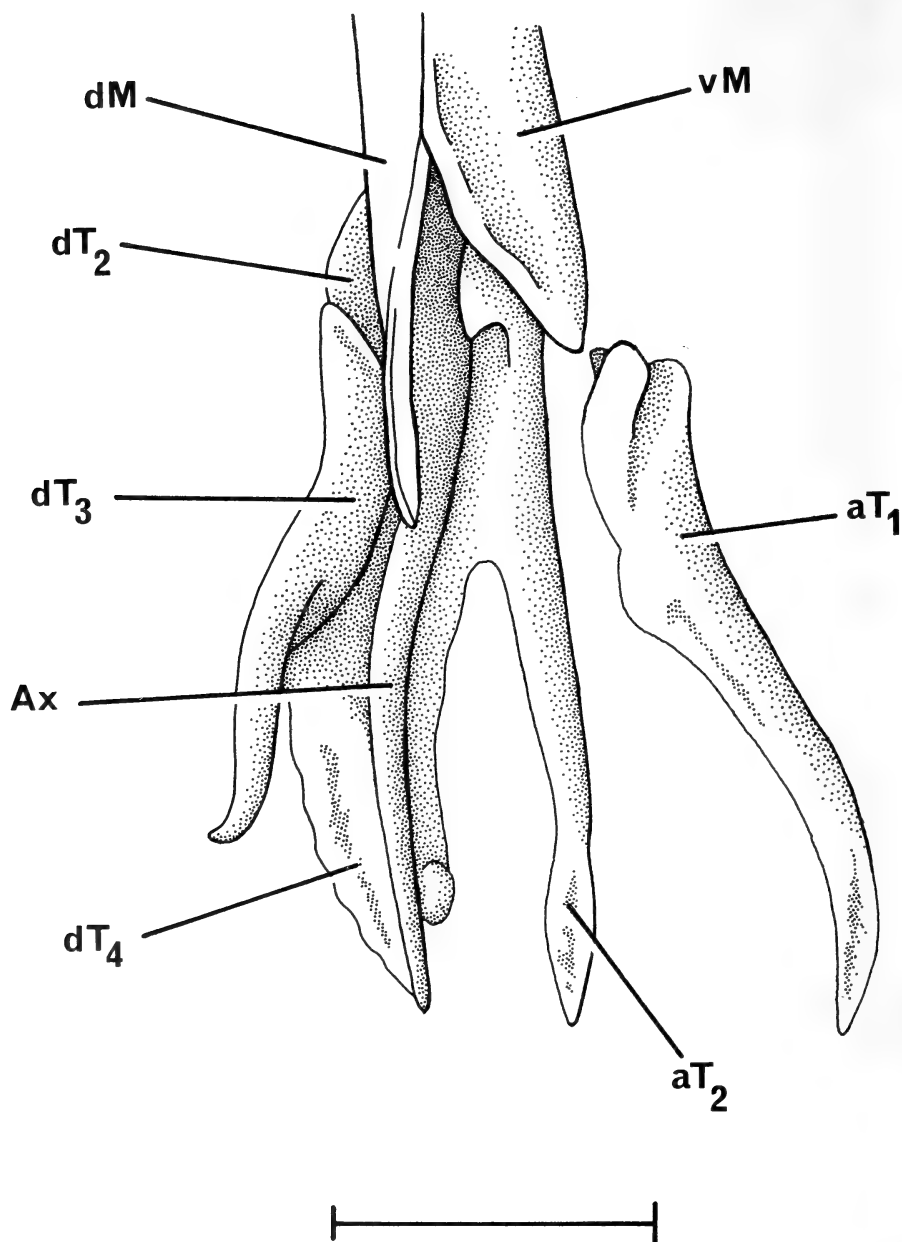


Fig. 6. *Springeria foliorostris*. Cartilages of right clasper with dT₁ and vT removed. Scale 10 mm.

lobe; inner dorsal lobe with proximal cleft and large fleshy palp, without a distal filament; rhipidion at level of hypopyle with pent extending distally from the rhipidion along inner lateral margin of shield; sentinel well developed and covered with pleated epithelia, partially covering spike; sentinel and spike situated medially.

Proximal cartilaginous elements (basal group): b_1 and b_2 cartilages, with covering β -cartilage arising from stepped axial to about one-half the length of the b_1 -cartilage. Four dorsal terminal cartilages: dT_1 plate-like, without a proximal shelf, situated entirely on dorsal side of organ, poorly calcified proximally; dT_2 comparatively small and connecting dM with dT_3 ; dT_3 well developed and projecting laterally outwards as a sharp point, the spur; dT_4 flat and poorly calcified, bonded to outer lateral edge of pointed Ax. vT dorsally concave with pointed distal tip and short anterior notch at about half the length of the cartilage. aT_1 comparatively narrow and elongate, with sharp-pointed, dorso-ventrally flattened tip. Bifurcate aT_2 , with spinal projection extending distally to a somewhat expanded, dorso-ventrally flattened blade-like tip, and with well developed attachment process arising at about one-third the length of the cartilage and tightly bonded to lateral edge of Ax.

Anacanthobatis longirostris (Figs 7, 8, 9)

Clasper comparatively short with naked, slightly expanded and dorso-ventrally flattened tip; pseudosiphon absent; spur well developed, forming outer lateral margin of dorsal lobe with palp; inner dorsal lobe with proximal cleft; slender palp arising at level of rhipidion, with a short distal filament; rhipidion at level of hypopyle, without a pent; shield dorsally convex and distally truncate, without laminate integument; sentinel with sharp point and covered basally with pleated integument, partially overlying spike; sentinel and spike situated medially.

Proximal cartilaginous elements (basal group): b_1 and b_2 cartilages with dorsally situated β -cartilage, arising from stepped Ax to about one-half the length of b_1 -cartilage. Four dorsal terminal cartilages: dT_1 without proximal shelf but with distal point, situated dorsally but with inner lateral edge curved to wrap around Ax on to ventral side; dT_2 comparatively small and comma-shaped, connecting dM with dT_3 ; dT_3 asymmetrical proximally and broadly expanded distally, with sharp-pointed, Z-shaped outer lateral projection, the spur, and short, truncate, inner lateral extension; dT_4 shield-like and poorly calcified, with proximal inner extension fusing with dT_3 . vT simple, dorsally convex with truncate distal tip and with short anterior notch at about one-half the length of the cartilage. aT_1 dorso-ventrally flattened with condyle-like proximal end and slightly expanded, knife-like distal point. Bifurcate aT_2 , with spinal projection extending distally to somewhat expanded, dorso-ventrally flattened, blade-like tip, and with well developed attachment process, arising at about one-third the length of the cartilage, tightly bonded to lateral edge of Ax.

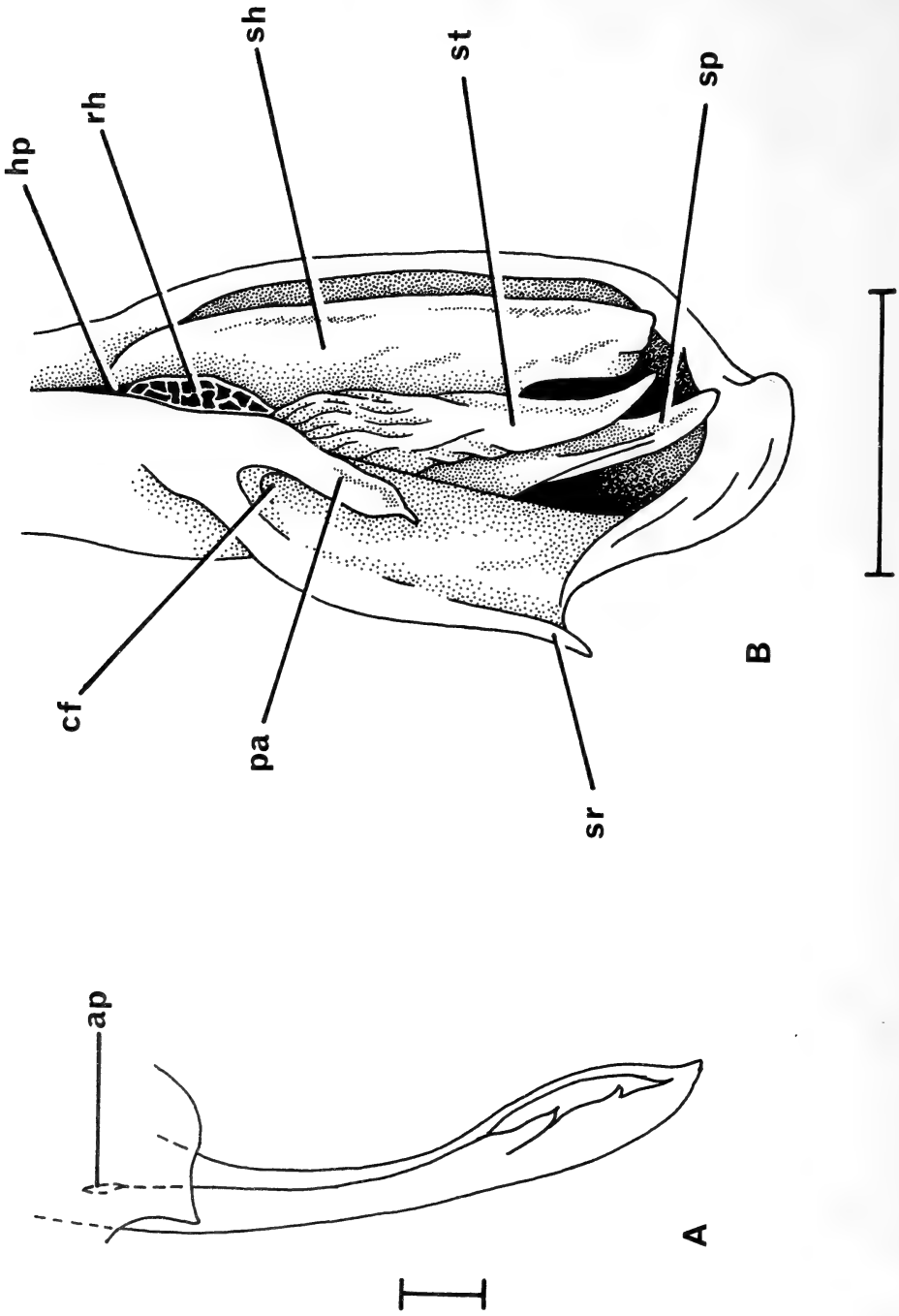


Fig. 7. *Anacanthobatis longirostris*. A. external view of right clasper from the dorsal side. B. lateral view of right clasper opened to show structural features of the glans. Scale 10 mm.
 ap—apopyle; cf—cleft; hp—hypopyle; rh—rhinophore; sh—shield; sr—spur; sp—spike; st—sentinel.

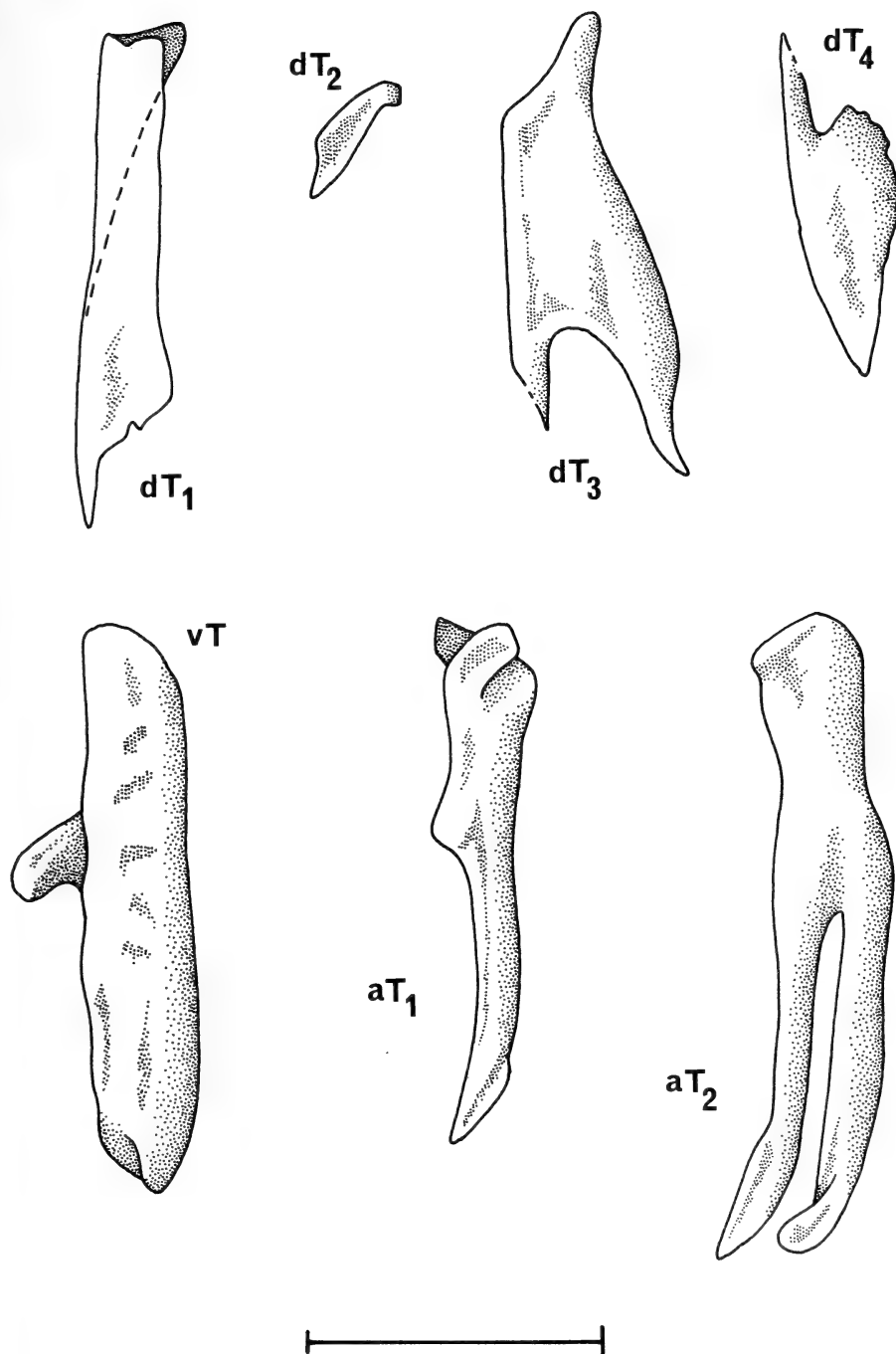


Fig. 8. *Anacanthobatis longirostris*. Terminal cartilages of the right clasper. dT₁, dT₂, dT₃, dT₄, vT—dorsal view; aT₁, aT₂—ventral view. Scale 10 mm.

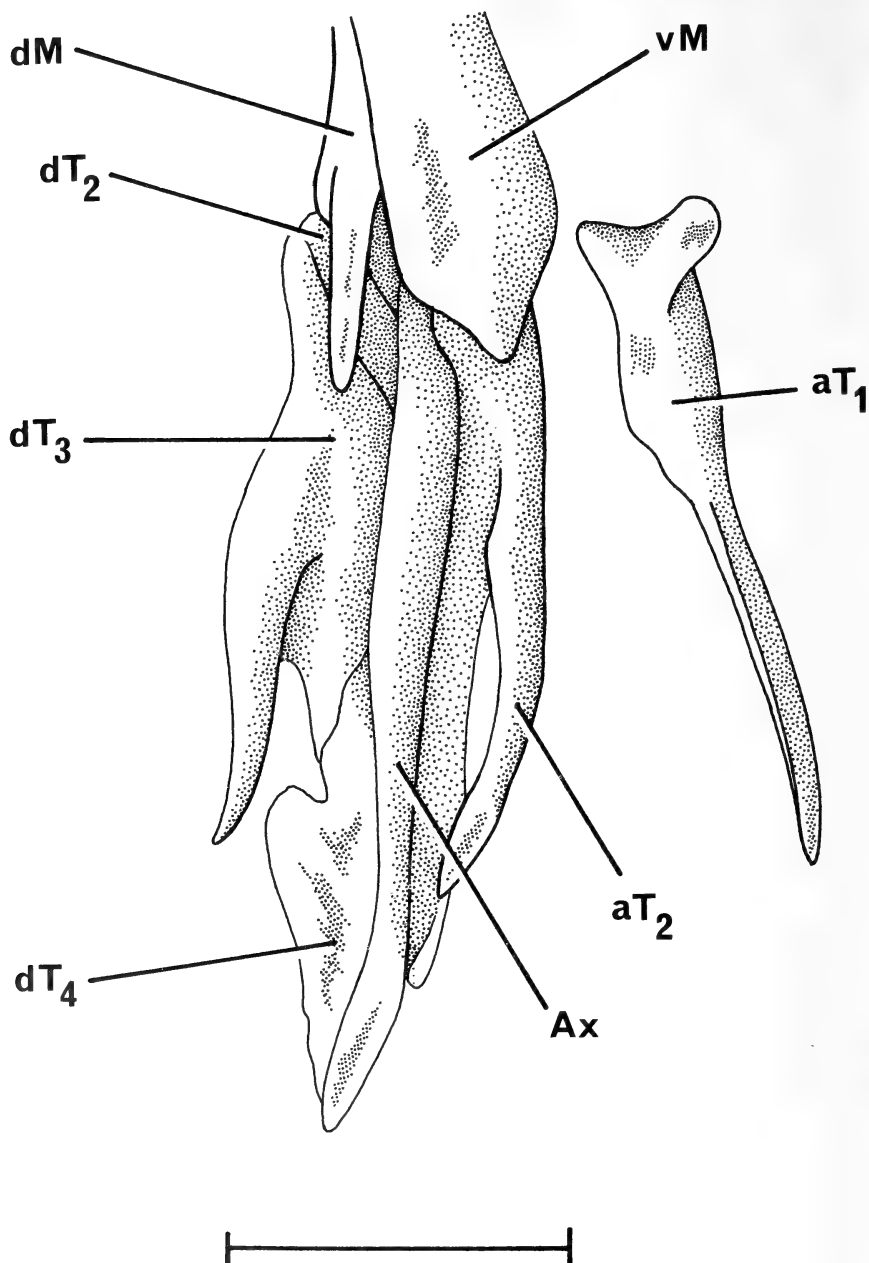


Fig. 9. *Anacanthobatis longirostris*. Cartilage of right clasper with dT_1 and vT removed. Scale 10 mm.

Anacanthobatis borneensis (Figs 10, 11, 12)

Claspers short with naked, slightly expanded and dorso-ventrally flattened glans; pseudosiphon, spur and palp absent; inner dorsal lobe with 2 proximal clefts; rhipidion at level of hypopyle; shield small, without pent; sentinel and, spike similar in size and shape, with dorso-ventrally flattened, blade-like tips situated laterally in glans; sentinel capable of rotation.

Proximal cartilaginous elements (basal group): b_1 and b_2 cartilages with dorsally situated β -cartilage arising from stepped Ax almost to b_1 /basipterygium junction. Two dorsal terminal cartilages: dT_1 absent, the *m. dilatator* inserting at proximal region of dT_3 ; dT_2 small and comma-shaped joining dT_3 with dM; dT_3 asymmetrical proximally with a small window, and distally elongated to form a straight, flat, lateral extension, which does not develop into a spur; short, inner lateral extension of dT_3 loosely connected with pointed Ax; dT_4 absent. vT expanded proximally to form a short shield, with elongate anterior notch situated at about one-third the length of the cartilage and wrapping around inner lateral margin of the organ on to the dorsal side; distal extremity of vT pointed and curving laterally inwards. Simply-pointed aT_1 with expanded joint-like proximal region. aT_2 asymmetrical, spinal process slightly Z-shaped with dorso-ventrally flattened blade-like tip; attachment process small and only slightly calcified, arising at about one-quarter the length of the cartilage and loosely bonded to lateral edge of Ax.

DISCUSSION

Consideration should be given to the fact that the number of species in the family Anacanthobatidae is small, so that further division into subgeneric groupings does not appear to serve a useful taxonomic purpose. However, within the Rajoidea, such subdivision serves not only for taxonomy but may also be employed in the construction and interpretation of phyletic relationships. It is within this context that the subgenera within the Anacanthobatidae will be considered.

There can be no doubt that a single family is involved in the cases of all described anacanthobatid species. All possess the U-shaped pelvic girdle characteristic of the Anacanthobatidae (Hulley 1972a). Furthermore, there are two proximal segments in the basal group of the clasper cartilages, which together with the presence of a pair of lateral prepelvic processes on the pelvic girdle, fully substantiate the inclusion of the family within the Rajoidea.

As already stated, the recognition of the genus *Springeria* is based solely on the terminal leaf-like expansion of the snout. The interpretation of this feature does not now appear to have been constant among the various authors of species in this genus (Bigelow & Schroeder 1951; Chan 1965a; Wallace 1967). The terminal expansion in *Springeria foliorostris* is well marked and is formed in an entirely different manner to the 'terminal expansion' in either *S. ori* or *S. melanosoma*. In these species, there is merely a blunt protuberance at the base

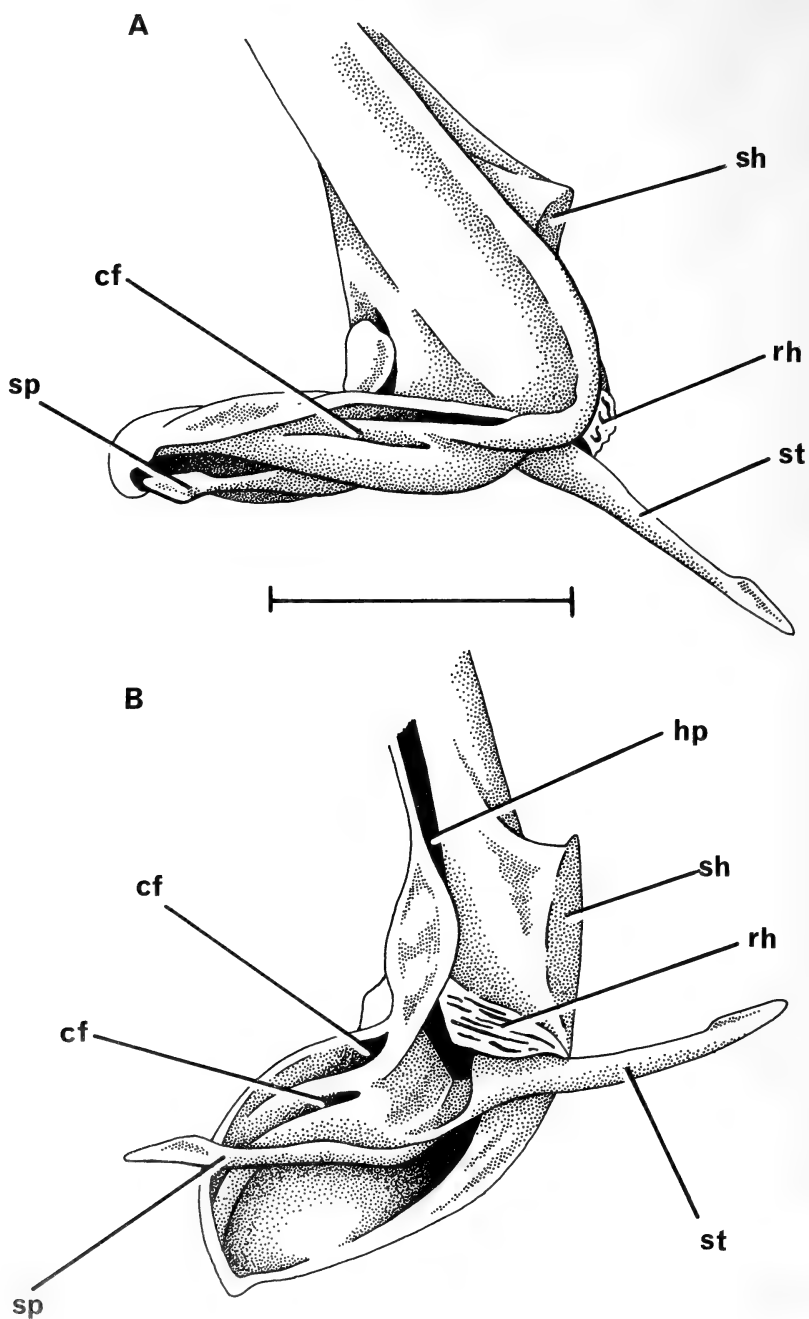


Fig. 10. *Anacanthobatis borneensis*. A. dorsal view of right clasper. B. lateral view of right clasper opened to show structural features of the glans. Scale 10 mm.

cf—cleft; hp—hypopyle; rh—rhipidion; sh—shield; sp—spur; st—sentinel.

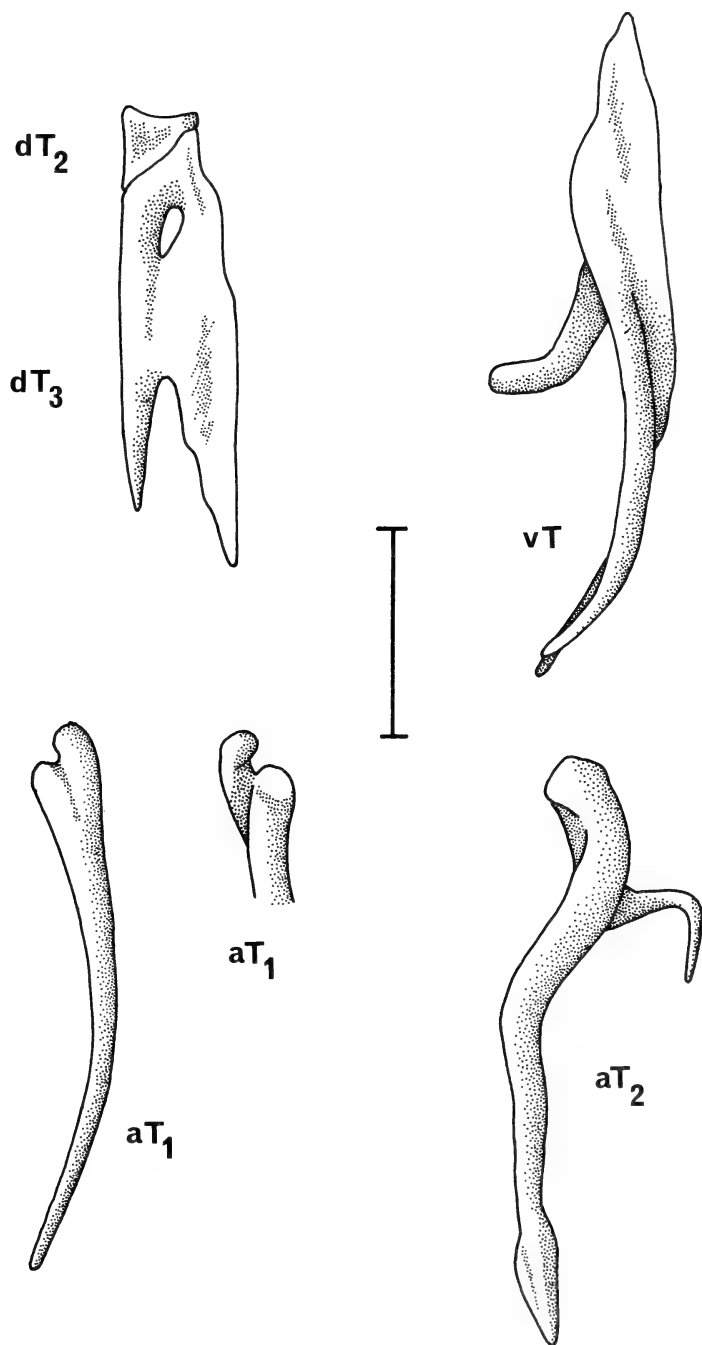


Fig. 11. *Anacanthobatis borneensis*. Terminal cartilages of the right clasper. dT₂, dT₃, vT, aT₁ (head only)—dorsal view; aT₁ (complete) aT₂—ventral view. Scale 5 mm.

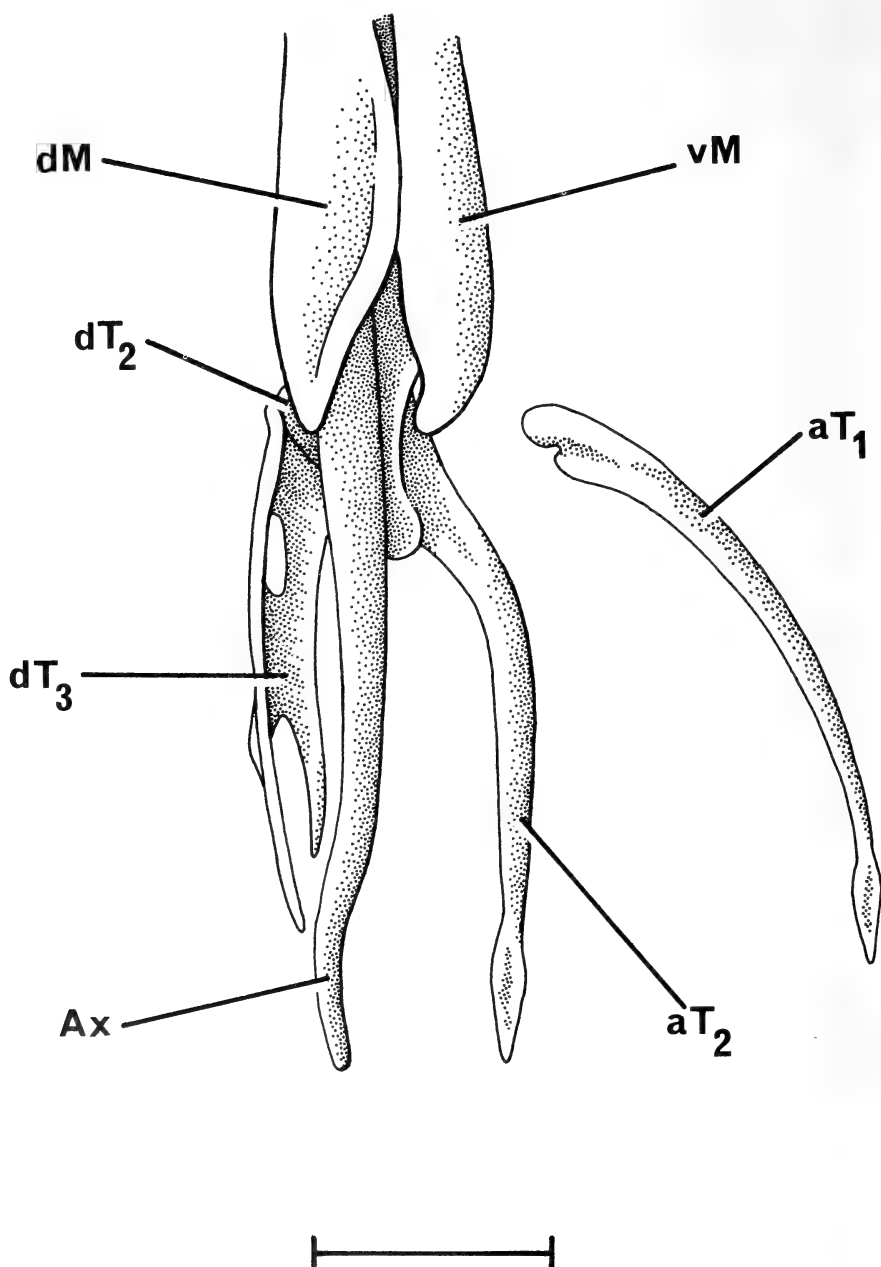


Fig. 12. *Anacanthobatis borneensis*. Cartilages of right clasper with vT only removed. Scale 5 mm.

of the rostral filament, a condition which is approximated in all anacanthobatid species including *S. foliorostris*. These facts, when considered in the light of the similarity in clasper structure of *Springeria foliorostris* and *Anacanthobatis longirostris* (Figs 4-9), indicate that the genus *Springeria* as based on this character is invalid, and that a terminal leaf-like expansion of the snout is a character applicable only at the species level to *S. foliorostris*.

This conclusion is further supported by the fact that the number of radials in both the pectoral and pelvic fins does not allow for the separation of *Springeria* as a separate genus. It appears that the number of mesopterygial radials in *Springeria foliorostris* is slightly higher than in other *Anacanthobatis* species. Unfortunately, counts of the number of mesopterygial radials in *S. ori* and *S. melanosoma* were not possible, due to the small degree of calcification of these cartilages.

X-ray examination has shown that unlike the Rajidae, the pectoral girdle in the Anacanthobatidae is sexually dimorphic. In males the propterygium consists of two articulated segments, while in females there is a single propterygial element (Fig. 13). In rajids two articulated propterygial elements are found in both sexes. The comparative size of the mesopterygium varies in different species, but its use as a specific, subgeneric or generic diagnostic character is difficult to assess at this stage.

To summarize, the genus *Springeria* cannot be distinguished from *Anacanthobatis*; the terminal leaf-like expansion of the snout is applicable only to *S. foliorostris* and lends itself as a diagnostic character at the species level.

On the basis of the external and internal anatomy of the claspers, the characters of which appear to be the most reliable criteria in the taxonomy of the Rajoidea, the following species of *Anacanthobatis* are now distinguished: *A. marmoratus*, *A. americanus*, *A. longirostris*, *A. borneensis* and *A. foliorostris*.

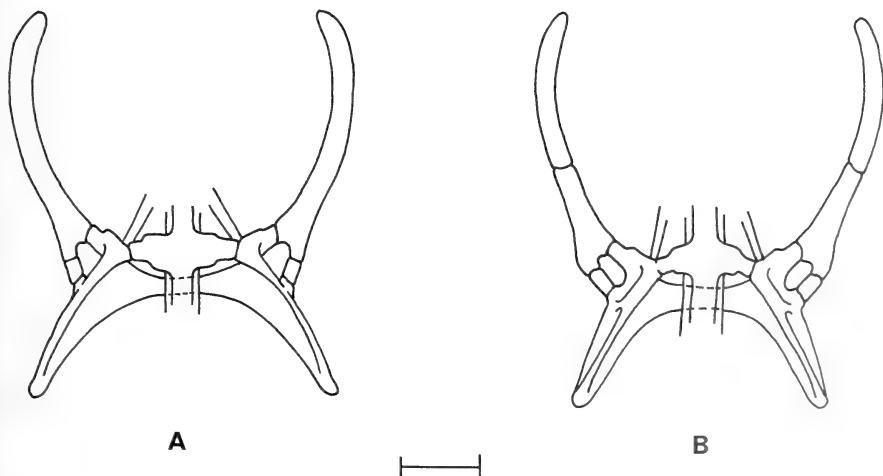


Fig. 13. Pectoral girdles of *Anacanthobatis marmoratus*. A. female; B. male. Scale 10 mm.

Anacanthobatis ori appears to resemble *A. marmoratus* in the complete fusion of the inner margin of the pelvic fin with the base of the tail, a character which is unique to these two species. However, for the moment, *Anacanthobatis ori* is retained as a separate species on the basis of a lower teeth count (20–24 rows in upper jaw in *A. ori*; 32–35 rows in *A. marmoratus*), a comparatively longer and more slender tail, larger eyes (which Wallace (1967) associates with the light intensity of a shallower depth habitat) and a nasal curtain which does not overlap the corners of the mouth. Similarly, *A. melanosomus* is retained for the moment as a separate species to the sympatric *A. borneensis* because of differences in the disc shape, snout length, tail length, nasal curtain and presence of minute thorns along the midline of the base of the tail (Chan 1965a, b). It should be noted that there is no difference in teeth count in these two species (24 rows in upper jaw). The low value of 14 rows in *A. melanosomus* reported by Chan (1965a) arises because the teeth are arranged in quincunx, but are widely separated. Since adult males of *Anacanthobatis ori* and *A. melanosomus* are unknown, it is impossible to comment on them further.

KEY TO SPECIES

- 1 (a) Dorsal surface of disc with dermal papillae 2
- (b) Dorsal surface of disc without dermal papillae 5
- 2 (a) Pelvics completely fused along entire length with root of tail 3
- (b) Pelvics not completely fused along entire length with root of tail 4
- 3 (a) 20–24 rows of teeth in upper jaw; nasal curtain not overlapping corners of mouth
A. ori
- (b) 32–35 rows of teeth in upper jaw; nasal curtain overlapping corners of mouth
A. marmoratus
- 4 (a) Length of tail from middle of vent greater than distance from middle of vent to base of rostral filament; interorbit about 3 in snout length to base of filament
A. melanosomus
- (b) Length of tail from middle of vent less than distance from middle of vent to base of rostral filament; interorbit about 7 in snout length to base of filament *A. borneensis*
- 5 (a) Length of snout about 4–5 times as long as diameter of eye *A. americanus*
- (b) Length of snout about 7–9 times as long as diameter of eye 6
- 6 (a) Snout with terminal leaf-like expansion; length of tail from middle of vent greater than distance from middle of vent to tip of snout *A. foliorostris*
- (b) Snout without terminal leaf-like expansion; length of tail from middle of vent less than distance from middle of vent to tip of snout *A. longirostris*

TAXONOMIC ARRANGEMENT OF THE ANACANTHOBATIDAE

On the basis of clasper structure, the family Anacanthobatidae can be taxonomically arranged as follows. It should be noted however that Hulley (1972a) has erroneously confused the sentinel/spike and aT_1/aT_2 in *Anacanthobatis americanus*.

Family **Anacanthobatidae**Genus *Anacanthobatis* Von Bonde & Swart, 1923type-species *Anacanthobatis marmoratus* Von Bonde & Swart, 19231. subgenus *Anacanthobatis* Von Bonde & Swart, 1923type-species *Anacanthobatis marmoratus* Von Bonde & Swart, 1923species: (?) *Anacanthobatis ori* (Wallace, 1967)—no adult male*Definition*

Claspers comparatively small, with spur on lateral dorsal border, but without pseudosiphon; inner dorsal lobe with proximal cleft and with slender proximal palp; palp without a terminal filament; rhipidion present; shield prominent with well developed eperon; sentinel and spike medially positioned; Ax spatulate; three dT elements, with spur developed from dT₃; vT proximally pointed with serrate outer lateral margin and with anterior notch well developed from windowed inner lateral margin; aT₁ distally spoon-shaped; aT₂ simply-pointed, attachment process absent.

2. subgenus *Springeria* Bigelow & Schroeder, 1951type-species *Anacanthobatis foliorostris* (Bigelow & Schroeder, 1951)species: *Anacanthobatis longirostris* Bigelow & Schroeder, 1962

In accordance with Article 67k of the International Code of Zoological Nomenclature, the name *Springeria* is retained, but is now redefined.

Definition

Claspers comparatively small, with spur developed on lateral dorsal margin but without pseudosiphon; inner dorsal lobe with proximal cleft and with proximal palp; palp with or without a distal filament; rhipidion present; shield well developed, eperon absent but pent present or absent; sentinel and spike positioned medially; Ax with pointed distal extremity; four dT elements, with spur developed from dT₃; vT simple and rounded proximally, with small anterior notch; aT₁ distally pointed or slightly blade-like; aT₂ with well developed blade-like spinal projection and well developed attachment process.

3. subgenus ***Sinobatis*** n. subgen.type-species *Anacanthobatis borneensis* Chan, 1965species: (?) *Anacanthobatis melanosomus* (Chan, 1965)—no adult male*Definition*

Claspers small, without spur on dorsal lateral margin and without pseudosiphon; inner dorsal lobe without palp but with two proximal clefts; rhipidion present; shield poorly developed laterally, but expanded medially to wrap

around Ax stem as small dorsal bump; sentinel and spike simple, with slight blade-like distal ends, situated laterally with sentinel capable of rotation; two dT cartilages, but dT₁ absent; spur not developed from distal projection of dT₃; Ax simply pointed distally; aT₁ simple with blade-like end; aT₂ with slender spinal projection and poorly developed attachment process.

4. subgenus *Schroederobatis* n. subgen.

type-species *Anacanthobatis americanus* Bigelow & Schroeder, 1962

Definition

Claspers small, with pseudosiphon in outer dorsal wall; spur absent; inner dorsal lobe without palp and cleft; rhipidion present; shield absent; sentinel and spike simple and positioned laterally, with sentinel capable of rotation; two dT cartilages with dT₁ well developed; Ax simply-pointed; vT absent; aT₁ and aT₂ similar in shape with slightly pointed, blade-like distal ends.

As has been pointed out, Hulley (1972a) has made tentative suggestions regarding the phylogenetic position of the Anacanthobatidae. He has proposed an early origin for the family, deriving it from the hypothetical *Dipturus* ancestral stock. This would mean therefore that certain characters of the Anacanthobatidae would also be exhibited by the Crurirajidae, *Dipturus*, *Amblyraja*, *Rajella* and *Leucoraja* species (Hulley 1972a: fig. 56).

The presence of an erectile rhipidion in all anacanthobatids, as well as the retention of the well developed distal projection to the dM, in the form of the palp, in *Anacanthobatis foliorostris*, *A. marmoratus* and *A. longirostris* (Figs 4, 7; Hulley 1972a: fig. 10) would substantiate this theory. However, the distal projection of the dM is not well developed in *A. americanus* and *A. borneensis* (Fig. 12; Hulley 1972a: fig. 11), but the lack of a vT and dT₁ respectively in these species, indicates a somewhat specialized condition of the claspers. This specialization is further emphasized by the arrangement and number of dT cartilages in *A. americanus* (Hulley 1972a: fig. 44), and by the peculiar development of the anterior notch of the vT in *A. borneensis* (Fig. 11).

The Crurirajidae might be considered to be directly ancestral to the Anacanthobatidae, since both families are characterized by the anterior limb-like lobe of the pelvic fin, and the absence of dorsal fins would then appear as a progression away from the crurirajid condition. Furthermore, the attachment process of the aT₂ in *Anacanthobatis* could then be interpreted as a development from the terminal bridge in *Cruriraja* (Hulley 1972a: figs 40, 41, 42). This terminal bridge links the aT₂ with the Ax. However, the position of the dT₁, nature of the Ax and typical condition of the aT₁ and aT₂ in *Cruriraja* preclude a direct development of the Anacanthobatidae from this family. Furthermore, an attachment process to the aT₂ is also developed in the *Rajella/Leucoraja/Amblyraja* line of evolution (Hulley 1972a: fig. 26).

A relationship with the *Amblyraja/Rajella/Leucoraja* line is further exemplified by the well developed dT₃ (spur) in almost all anacanthobatids, a frame-

work arrangement of the dT cartilages, the medial position of the anterior notch of the vT and the reduction in size of the dT₂. However, *Anacanthobatis* lacks the external pseudosiphon so typical of this group. The pseudosiphon in *Anacanthobatis americanus* (Hulley 1972a: fig. 11), although having a direct relationship with the dT₁, is not comparable to the form of this structure in *Amblyraja* and (?) *Rajella*.

To conclude, the Anacanthobatidae appear to have arisen separately from the same ancestral stock as both the Crurirajidae and the *Amblyraja/Rajella/Leucoraja* lines, and probably represent a direct modification of the *Dipturus* ancestral stock, which lost the pseudosiphon but retained the distal projection of the dM (palp) during the development of the rhipidion (Fig. 14). On the basis of clasper comparison therefore, the family does not now appear to have a diphyletic origin.

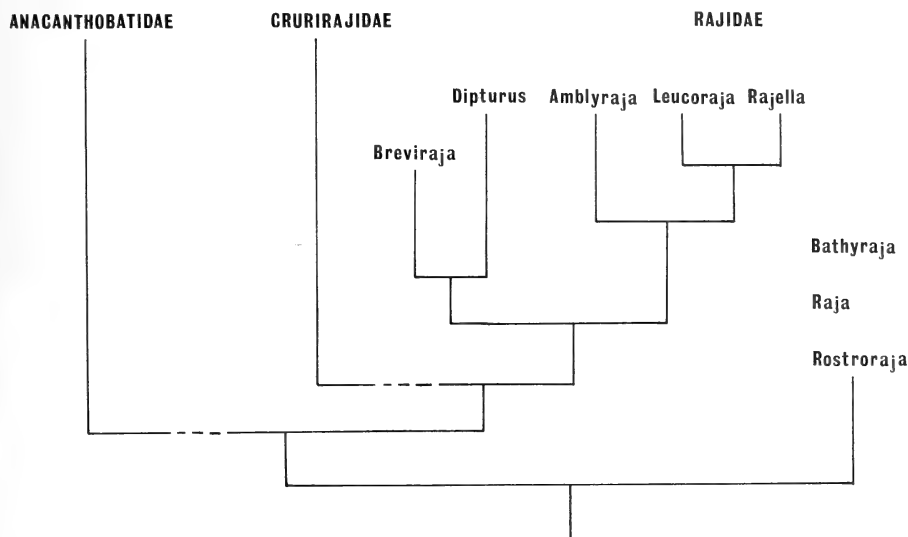


Fig. 14. Proposed phyletic relationships of the Anacanthobatidae.

Springeria probably represents the least specialized subgenus, closest to the basic ancestral stock, since the Ax is pointed, the distal end of the dM is well developed and the vT is relatively simple. Furthermore, the primitive condition of an elongate snout is retained, cf. *Dipturus* (Hulley 1972a). The anterior leaf-like expansion of the snout in *Anacanthobatis foliorostris* represents a direct modification of the condition in *A. longirostris* and would suggest a lesser age for *A. foliorostris*, a fact which is supported by the complete dorsal rotation of the dT₁.

The subgenus *Anacanthobatis* would then represent a split from the above condition, in which the snout was reduced, probably as an increased advantage in grubbing (Ishiyama 1958; Hulley 1972a). Further, there was a change in

form of the Ax and vT cartilages. The presence of a spatulate Ax, together with the loss of the dT₄ might be interpreted as a condition arising from the pointed Ax/plate-like dT₄ typical of *Springeria*. The windowing of the vT may represent the initial stages leading to the reduction (e.g. *A. borneensis*) and complete loss (e.g. *A. americanus*) of the vT. However, the retention of the primitively pointed Ax in these species precludes a direct modification of *Sinobatis* and *Schroederobatis* from *Anacanthobatis*.

Rather the complete loss of the vT, dT₃ and dT₄ cartilages in *Schroederobatis* represents a specialized condition, which may be associated with the lateral shift in position of aT₁ and aT₂. This suggestion may be valid if we consider that essentially the clasper of the male skate plugs the cloaca of the female. In *Schroederobatis* the dT₁ does not show complete dorsal rotation and, as has been pointed out above, the Ax retains its pointed condition, facts which suggest a specialization of the condition in *Springeria*.

Similarly, *Sinobatis* would represent a specialized condition arising from *Springeria*: the Ax is pointed and the dT₃ is comparatively well developed, although it does not manifest itself as a spur in the glans. Again the loss of the dT₁ may be associated with the lateral shift in position of the aT₁ and aT₂ cartilages, together with the peculiar development of the anterior notch of the vT, which runs around the Ax stem on to the dorsal surface of the glans.

It has already been suggested (Hulley 1972a, b) that the Crurirajidae and *Breviraja* may have had their origin in the waters of the central western Atlantic and may have spread from this area to the southern African region at a later date. On the evidence presented above, this would also seem to be the case in the Anacanthobatidae, since not only are the most primitive forms known from the western central Atlantic but this region also shows the greatest species diversity of Anacanthobatidae.

SUMMARY

The lectotype of *Anacanthobatis marmoratus* Von Bonde & Swart, 1923 is designated and described.

The pelvic girdles, rostral filaments, pectoral and pelvic radials of the Anacanthobatidae and the clasper structure of *Anacanthobatis longirostris*, *A. borneensis* and *Springeria foliorostris* are described.

On the basis of the above, it appears that the anterior leaf-like expansion of the snout is present only in *S. foliorostris* and is valid only as a diagnostic character at the species level. The genus *Springeria* is taxonomically invalid at the generic level, and all species should be referred to the genus *Anacanthobatis*. A key to the species is given.

Since there are relatively few species involved in the family Anacanthobatidae, further division into subgenera does not serve a useful taxonomic purpose. However, for interpretation of the phylogeny of the family, subgeneric groupings, based on the clasper structure, have been constructed as follows:

Family **Anacanthobatidae**Genus *Anacanthobatis* Von Bonde & Swart, 1923type-species *Anacanthobatis marmoratus* Von Bonde & Swart, 19231. subgenus *Anacanthobatis* Von Bonde & Swart, 1923type-species *Anacanthobatis marmoratus* Von Bonde & Swart, 1923species: (?) *Anacanthobatis ori* (Wallace, 1967)2. subgenus *Springeria* Bigelow & Schroeder, 1951type-species *Anacanthobatis foliorostris* (Bigelow & Schroeder, 1951)species: *Anacanthobatis longirostris* Bigelow & Schroeder, 19623. subgenus ***Sinobatis*** n. subgen.type-species *Anacanthobatis borneensis* Chan, 1965species: (?) *Anacanthobatis melanosomus* (Chan, 1965)4. subgenus ***Schroederobatis*** n. subgen.type-species *Anacanthobatis americanus* Bigelow & Schroeder, 1962

In accordance with Article 67(k), of the International Code of Zoological Nomenclature, *Springeria* is retained as a subgenus, but is redefined.

The phyletic interrelationships of the family are discussed in terms of these morphological details and an evolutionary pattern is proposed. On this evidence it seems likely that, as in the case of the Crurirajidae and of *Breviraja*, the Anacanthobatidae had their origin in the central western Atlantic.

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FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Etudes sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627-634.

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P. A. Hulley

INTERRELATIONSHIPS WITHIN
THE ANACANTHOBATIDAE
(CHONDRICHTHYES, RAJOIDEA),
WITH A DESCRIPTION OF THE LECTOTYPE OF
ANACANTHOBATIS MARMORATUS
VON BONDE & SWART, 1923

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A NEW SPECIES OF *PARAMELITA*
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FROM SOUTH AFRICA

By
MICHAEL H. THURSTON

Cape Town Kaapstad

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By

MICHAEL H. THURSTON

Institute of Oceanographic Sciences, Wormley, Godalming, Surrey, England

(With 3 figures)

[MS. accepted 25 April 1973]

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INTRODUCTION

In his major contribution to the amphipod fauna of South Africa, Barnard (1916) assigned to the genus *Gammarus* four new species from fresh-water localities in the Cape Peninsula. These records were the first of fresh-water amphipods from South Africa, and with the exception of *Gammarus pulex* (L.) as noted by Krauss (see Stebbing 1910: 456), the first record of the genus from South Africa. Schellenberg (1926) erected the genus *Paramelita* for the new species *P. ctenodactyla* described from material collected by the Deutsche Süd-polar-Expedition. In the following year, Barnard published results obtained from collections made in fresh-water localities in the south-western part of the Cape Province (Barnard 1927). Although Barnard was able to equate *P. cteno-dactyla* with *Gammarus capensis* Barnard, 1916, he found it necessary to erect a further six species, thus raising to ten the number of *Gammarus* known from fresh-water localities in South Africa. Schellenberg (1937) showed that the South African species assigned to *Gammarus* were sufficiently distinct from those of Palaearctic and Nearctic Regions to warrant generic separation, and so transferred them to *Paramelita*.

In 1970 I received from Miss Mary Hazleton, Honorary Biological Recorder of the Cave Research Group of Great Britain, a small collection of amphipods which, among the European material, contained two specimens from South Africa. This material clearly belonged to the genus *Paramelita*. A comparison with syntype material of most of the species described by Barnard, which had been deposited at the British Museum (Natural History) in 1928, precluded the present specimens from any of these species. The two specimens are therefore described herein as a new species, *Paramelita barnardi* sp. nov.

The species is dedicated to the late K. H. Barnard in recognition of his significant contributions to the knowledge of the fauna of South Africa and of tropical and Southern Hemisphere amphipods.

MATERIAL

The holotype, a 9 mm male, has been deposited in the collection of the British Museum (Natural History) under the registration number 1972:542:1, and the allotype, a 9 mm female, is registered in the collection of the South African Museum under number S.A.M. A13199.

Both specimens were collected from Boomslang Cave, Cave Peak, above Kalk Bay, near Cape Town, South Africa. They were found by M. Ware in a small muddy pool in the dark zone on 23 June 1969.

DESCRIPTION

The description is based on the holotype, which differs from the allotype only in minor details of setation and spination. Body moderately compressed, peraeon five fourths length of pleon. *Peraeon*, coxae 1 to 4, depth a little less than corresponding segments, segments 2 to 7 bearing branchiae, those of segment 7 the smallest. Accessory branchiae present on peraeon segments 2 to 7; one on segments 2 and 3, two on segments 4, 5 and 7 and four on segment 6. *Pleon* segments with setae dorsally, segments 1-3 each with 6-7 setae at posterior margin, segments 4 and 5 with 2-4 setae on posterior margin and paired groups of 5-6 setae a little anterior and lateral to the mid-point of the posterior margin; segment 6 similar to 4 and 5 but with a spine and 3 setae in each lateral group. *Epimeron* 1, distally rounded, posterior margin convex and armed with ca 12 short, fine setae set in minute notches; two ranks of ten and six setae exteriorly just above distal margin. *Epimeron* 2, deeper than epimeron 1, distally rounded; posterior margin barely convex, armed with fine setae; five ranks of 7, 13, 15, 6 and 13 setae above distal margin; a spine among the setae of the third rank. *Epimeron* 3, similar to second but a little broader; setae on posterior margin less regularly spaced; six ranks of 7, 8, 12, 2, 10 and 9 setae above distal margin; first two ranks also contain single spines.

Head longer than first peraeon segment; rostrum obsolete, eye lobe deep, but not sharply produced, broadly rounded above, obtusely angled below; post-antennal angle sub-acute with 3-4 short setae anteriorly; margin between eye lobe and post-antennal angle excavate to accommodate inflated basal article of antenna 2; epistome straight, not protruding beyond upper lip; eye small, unpigmented in alcohol, apparently degenerate and lacking ommatidia. *Antenna* 1, length equal to that of head and peraeon segments 1 to 6 combined; lengths of peduncle articles in ratio 3:2:1; flagellum of 35 articles, just more than twice length of peduncle, each article with several short, fine setae, disto-ventrally; accessory flagellum of 5 articles, just shorter than article 2 of peduncle. *Antenna* 2, $\frac{5}{6}$ length of antenna 1; article 1 of peduncle inflated,

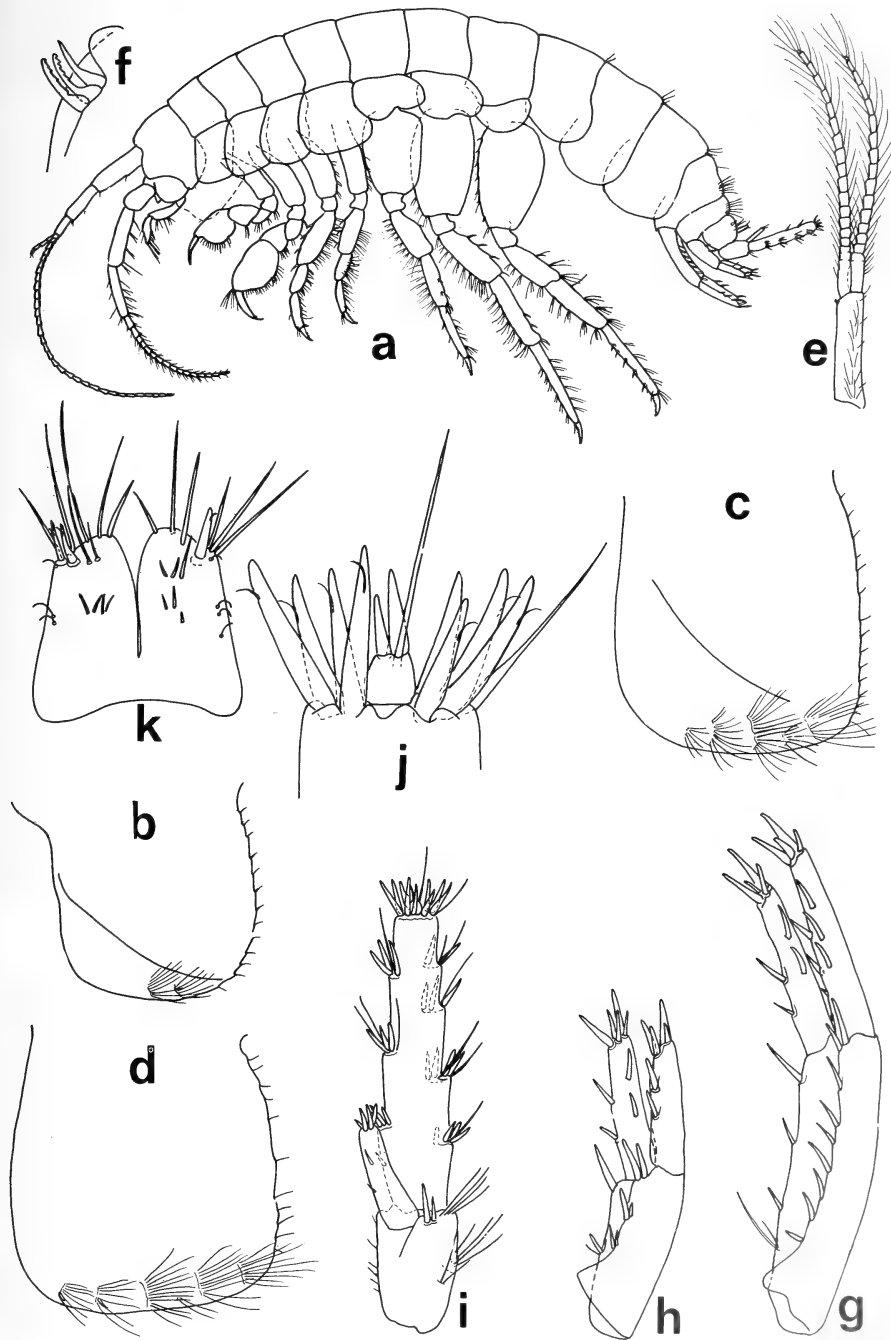


Fig. 1. *Paramelita barnardi* sp. nov.

a. Habitus. b. Epimeron 1. c. Epimeron 2. d. Epimeron 3. e. Pleopod 1. f. Locking spines of pleopod 1. g. Uropod 1. h. Uropod 2. i. Uropod 3. j. Second article of outer ramus of uropod 3.

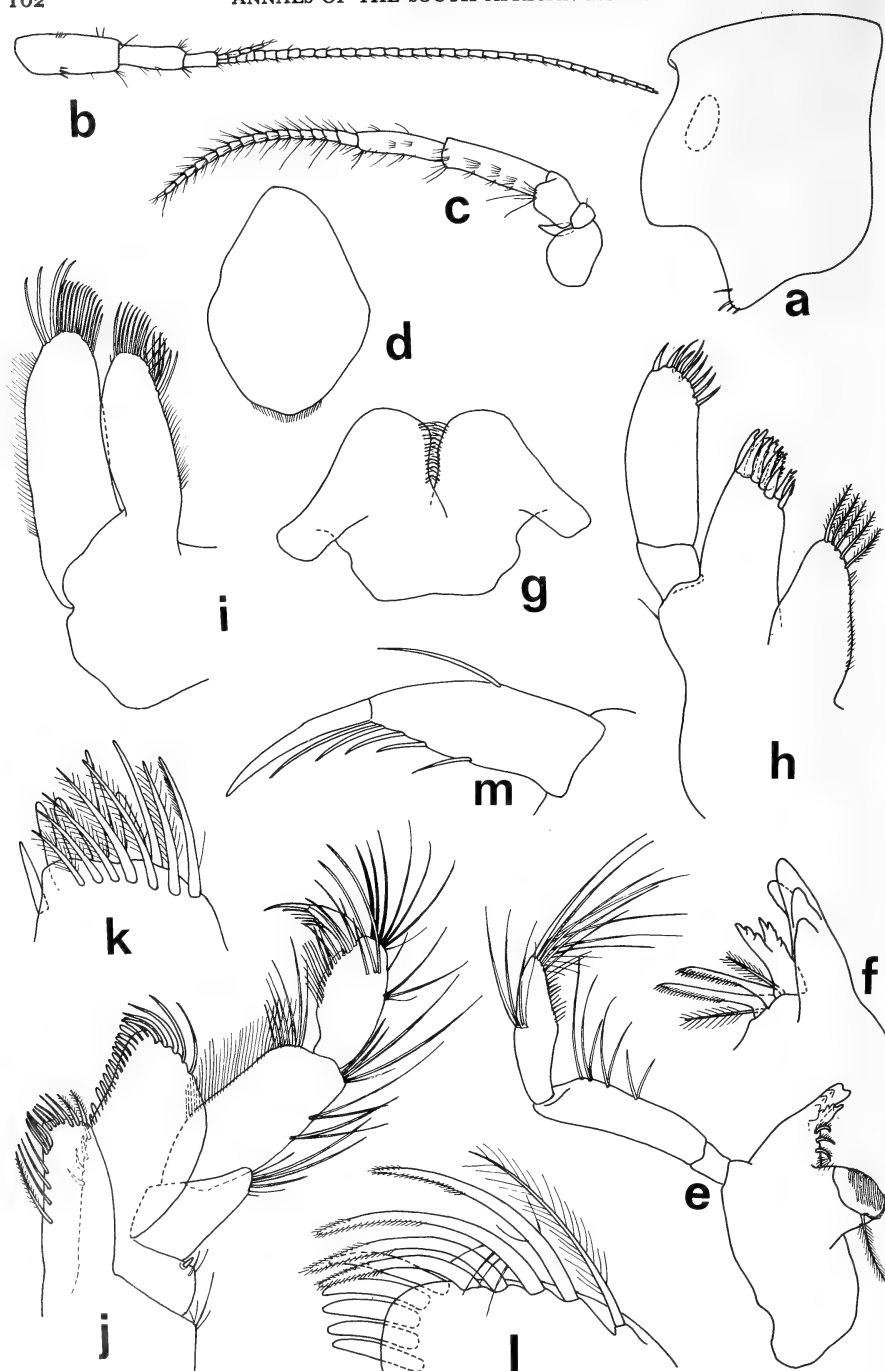


Fig. 2. *Paramelita barnardi* sp. nov.

a. Head, b. Antenna 1. c. Antenna 2. d. Upper lip. e. Left mandible. f. Apex of right mandible. g. Lower lip. h. Maxilla 1. i. Maxilla 2. j. Maxilliped. k. Inner plate of maxilliped. l. Outer plate of maxilliped. m. Dactyl of palp of maxilliped.

broadly ovoid, article 4 stouter than and $\frac{1}{5}$ longer than fifth article; flagellum $\frac{2}{3}$ to $\frac{3}{4}$ length of peduncle, of 17 articles, each article bearing groups of graded setae anteriorly and posteriorly close to the distal margin. *Upper lip* rounded, distally setose. *Left mandible*, incisor process bluntly five-toothed; lacina mobilis with four blunt teeth; spine row consisting of three hooked spines, each strongly and bilaterally pectinate; molar cylindrical, triturating surface oblique, armed with ridges and teeth and with a long plumose seta proximally at the edge of the triturating surface; palp rather longer than body of mandible; first article just longer than wide; second much longer than first, with seven setae on distal half of slight anterior expansion; third article narrowly pyriform, $\frac{5}{8}$ length of second article, anterior half of margin naked, distally armed with row of short, sharp setae, and terminal $\frac{1}{4}$ bearing *ca* 14 long, stout setae in two parallel rows. *Right mandible*, differs from left in having the incisor process with four blunt teeth, lacina mobilis bifurcate, each branch bearing four sharp teeth and spine row of two straight, stout, unilaterally pectinate spines and two plumose setae. *Maxilla 1*, inner plate triangular, apex subacute and bearing five plumose setae, inner margin pubescent; outer plate with 10 to 11 stout, toothed spines distally; palp, moderately broad, second article with broadly rounded apex armed with eight spines and two subapical setae on posterior margin. *Maxilla 2*, inner plate a little shorter and narrower than outer, apex broadly rounded, two ranks of setae, one apical and the other subapical, just extend on to inner margin, inner margin proximally pubescent; outer plate with broadly rounded apex bearing row of *ca* 15 setae, the posterior surface bears a submarginal row of 11 long stout setae just below the apex. *Lower lip*, inner lobes absent, outer lobes strongly setose on inner margin, mandibular process well developed. *Maxilliped*, inner plate apically truncate, armed with three stout and two slender spines at the apex and a subapical row of seven plumose setae which is contiguous with the row of ten plumose setae on inner margin; outer plate longer than inner, extending to $\frac{3}{8}$ length of palp article 2, rounded apex with five long curved pectinate spines, inner margin with *ca* 16 stout, blunt and closely set spine teeth; palp article 2 the longest, second and third articles densely setose medially; dactyl rather slender with five setae on medial margin, unguis forming nearly half of total length.

Gnathopod 1, coxa rectangular, distal margin setose; basal longer than depth of coxa, carpus and propod subequal, together as long as basal; propod distally expanded, length $\frac{3}{2}$ of breadth, palm gently convex, as long as posterior margin, armed with *ca* 25 setae of various lengths; palmar angle with 5 spines; dactyl as long as palm. *Gnathopod 2*, coxa slightly narrowed distally, rather longer than coxa 1, distally setose; carpus and propod combined a little longer than basal; propod nearly twice as long as carpus, otherwise similar to gnathopod 1. *Peraeopod 3*, coxa similar in form to that of gnathopod 2, but a little deeper, depth just greater than length: basal $\frac{4}{5}$ length of coxa; article 4 $\frac{5}{8}$ length of basal, equal to carpus and propod combined, length four times breadth, somewhat expanded, strongly setose posteriorly and with three groups of spines

and setae anteriorly; carpus more slender than merus, stouter and just shorter than propod, carpus and propod strongly armed with spines and setae posteriorly; dactyl half length of propod, somewhat hooked, with three spine setae posteriorly. *Peraeopod 4*, coxa rectangular, height and length subequal, shallowly excavate posteriorly, posterior angle obtuse, setose on posterior and posterior-ventral margins; distal articles similar to, but slightly shorter than those of peraeopod 3. *Peraeopod 5*, coxa, longer than deep, bilobed, anterior lobe the deeper, three short setae on posterior margin, basal expanded posteriorly, breadth $\frac{2}{3}$ of length, posterior distal lobe rounded, weak, anterior margin armed with spines and setae, posterior margin with *ca* 18 short fine setae; merus $\frac{3}{4}$ length of basal, rather stout, strongly setose anteriorly, a single stout spine on posterior margin; carpus and merus subequal, but former only half width of latter, armed with setae on anterior margin and spines posteriorly; propod subequal in length, but more slender than carpus, armed with spines anteriorly and setae posteriorly; dactyl apically hooked, with six spine setae anteriorly. *Peraeopod 6*, *ca* $\frac{4}{5}$ length of peraeopod 5, coxa weakly bilobed, three short setae on margin above posterior-distal angle; basal expanded, breadth $\frac{3}{4}$ of length, posterior distal lobe rounded, weak, anterior margin with spines and setae, posterior margin just concave, lined with 22 fine setae; merus $\frac{2}{3}$ length of basal, length three times breadth, strongly setose anteriorly, two stout spines posteriorly; carpus subequal in length to merus, but more slender, strongly armed anteriorly with spines and setae; propod a little shorter than basal, rather slender, breadth less than $\frac{1}{6}$ of length, strongly spinous anteriorly and with many setae posteriorly; dactyl $\frac{1}{3}$ length of propod, similar in form to that of peraeopod 5. *Peraeopod 7*, just shorter than peraeopod 6; coxa semicircular, setose on posterior $\frac{1}{3}$ of free margin; basal expanded, distinctly tapering distally, posterior-distal lobe obsolete, armed with spines and setae anteriorly and short setae posteriorly; merus rather stout but not strongly produced distally; carpus $\frac{4}{5}$ length of merus, breadth $\frac{2}{3}$ of length; propod $\frac{1}{6}$ longer, but more slender than carpus; merus, carpus and propod densely clothed with spines and setae anteriorly, less so posteriorly, dactyl $\frac{1}{3}$ length of propod, structure as in peraeopods 5 and 6.

Pleopods are fully developed, rather slender, length of peduncle four times breadth, setae of rami rather short. *Uropod 1*, rather stout, dorso-lateral margins of peduncle with nine spines, dorso-medial margin with three; rami subequal, $\frac{2}{3}$ length of peduncle, outer ramus with three spines on each margin, inner ramus with three on outer margin and two on inner, each ramus with two long and three shorter apical spines. *Uropod 2*, short, stout, extending posteriorly only as far as apices of uropod 1; peduncle with three pairs of spines on outer margin and two single spines on inner; inner ramus $\frac{5}{8}$ length of peduncle with two spines on each margin; outer ramus $\frac{3}{4}$ length of peduncle with two and one spines on outer and inner margins respectively; each ramus with five apical spines. *Uropod 3*, peduncle short, stout, breadth *ca* $\frac{3}{8}$ of length; inner ramus short, tapering distally, length $\frac{1}{6}$ of peduncle, lateral spines zero and two respec-

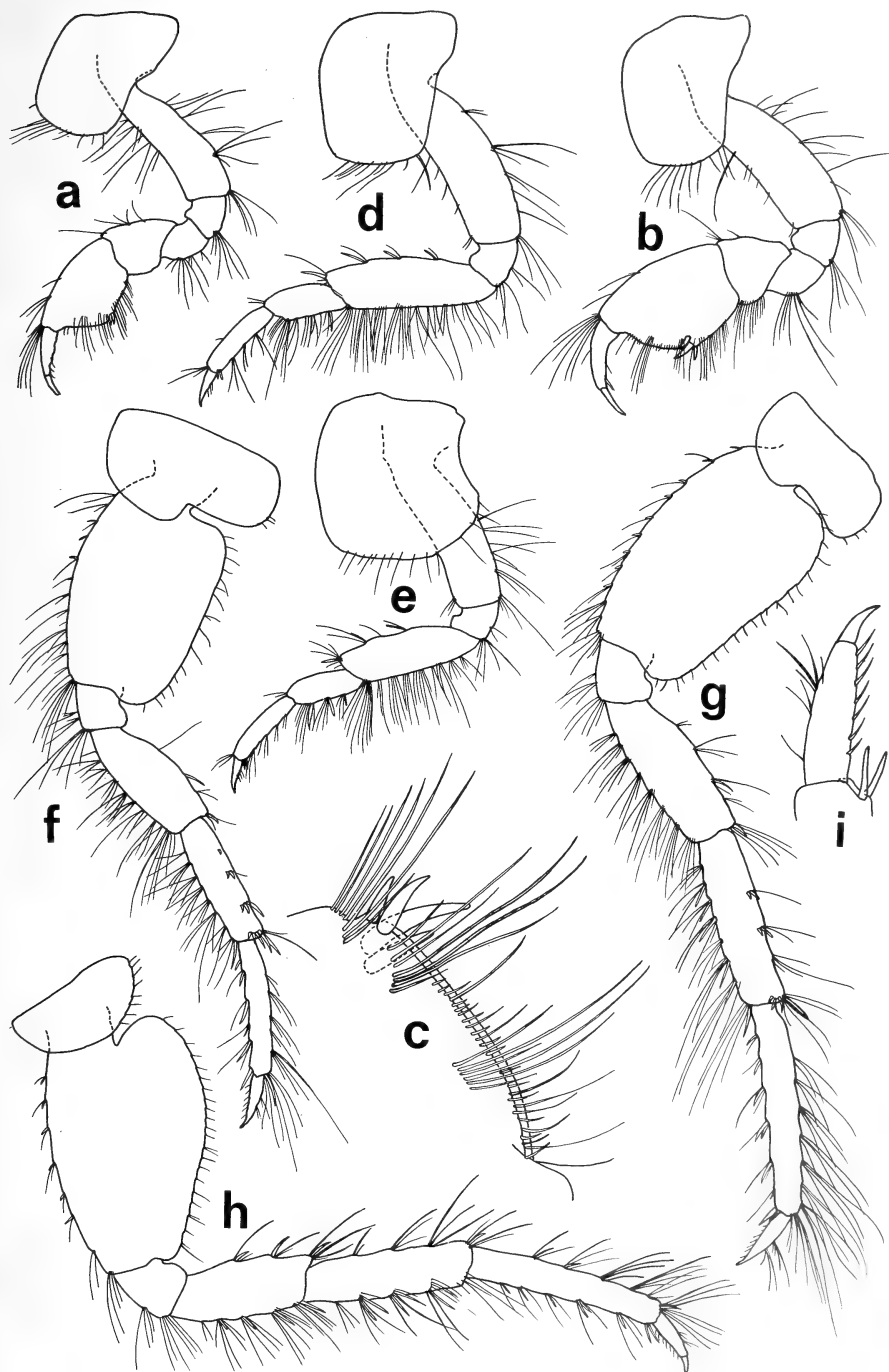


Fig. 3. *Paramelita barnardi* sp. nov.

a. Gnathopod 1. b. Gnathopod 2. c. Palm of gnathopod 2. d. Peraeopod 3. e. Peraeopod 4.
f. Peraeopod 5. g. Peraeopod 6. h. Peraeopod 7. i. Dactyl of peraeopod 7.

tively, apically four spines and two setae; first article of outer ramus much longer than inner, length more than twice that of peduncle, breadth $\frac{1}{4}$ of length, laterally strongly armed with $4 + 4$ groups of stout spines and some setae, apex truncate with corona of ten stout spines; second article very short, ca $\frac{1}{15}$ length of first article, apically with two spines and a seta, length of second article together with apical spines not exceeding that of apical spines of first article. *Telson*, rather broader than long, cleft $\frac{4}{5}$ length, lobes a little dehiscent distally; apices irregularly rounded, armed with one or two apical spines and four or five apical or subapical setae, dorsal surface with four to six short setae asymmetrically arranged and two or three short plumose setae close to the lateral margin of each lobe.

DISCUSSION

The genus *Paramelita* in South Africa consists of a closely related group of species some of which show curious morphological modifications involving the peduncle of antenna 2 and, in one case, pereopod 3. These variations are fully developed only in adult males, but are usually distinguishable in a weaker form in immature males. Differences between females of the various species are more subtle. Apart from antenna 2 and pereopod 3, some degree of sexual dimorphism is usually apparent in the gnathopods, although this is rarely as obvious as is the case in many European species belonging to *Gammarus* and allied genera.

Paramelita barnardi is characterized by the following attributes: medium size, unpigmented eyes, unmodified male antenna 2, oblique palmar margins and the relative size of propods of gnathopods 1 and 2, unmodified male pereopod 3, rectangular and weakly excavate coxa 4, strongly spinose and setose pereopods 5-7, and minute second article of uropod 3.

The weakly excavate coxa 4 of *P. barnardi* distinguishes this species from *P. capensis* and *P. nigroculus*. *P. capensis* also differs in having more broadly expanded basal articles of pereopods 5-7 and setose rather than spinose uropod 3. Additional characters separating *P. nigroculus* from *P. barnardi* are the pigmented eye, slender gnathopod 2 propod and acutely produced posterior-distal angle of epimeron 3 of the former. Epimera 3 of *P. nigroculus* var. *persetosus* more nearly resemble those of *P. barnardi* than the typical variety, but the marked difference in the degree of setal armature of antenna 2 affords an additional character by which the new species can be distinguished.

P. auricularis, *P. crassicornis*, *P. seticornis*, *P. spinicornis* and *P. tulbaghensis* are all characterized by modifications of the peduncle of antenna 2 in the male, whereas in *P. barnardi* the male antenna 2 does not differ from the condition found in the female. The bizarre subchelate condition of the male pereopod 3, nearly transversely palm of gnathopod 2 and narrow basal article of pereopod 7 also distinguish *P. auricularis* from *P. barnardi*. Pereopods 5-7 of *P. crassicornis* are shorter, stouter and less setose than those of the new species which can also

be distinguished by the oblique palmar margins of the gnathopods. The forms of both pairs of gnathopods are also additional characters separating *P. seticornis* from *P. barnardi*. The relatively slender propods of gnathopods 1 and 2 and the deep coxa 4 are features which separate *P. spinicornis* and the present species. Additional characters distinguishing *P. tulbaghensis* from *P. barnardi* are the strongly produced eye lobe, elongate first peduncle article of antenna 1, short convex palm of gnathopod 2 and narrow basal articles of pereopods 6 and 7 of the former species. *P. granulicornis* has a strongly convex palm on gnathopod 2, unexcavate coxa 4, and a distally expanded merus on pereopods 3 and 4. In the key to *Paramelita* species given by Barnard (1927: 167) the species described herein keys down to the couplet separating *P. kogelensis* and *P. aurantius*, and it is to these two species that *P. barnardi* appears most closely related. Both of these species are smaller than *P. barnardi*. *P. kogelensis* can be separated from *P. barnardi* by the rather strongly setose flagellum of antenna 1, the shorter palm of gnathopod 2, the form of coxa 4, and the presence of a small blunt tooth at the posterior-distal angle of epimeron 3. *P. aurantius* is distinguished from *P. barnardi* by the relatively greater disparity in size between gnathopods 1 and 2, the more nearly transverse palms of these appendages and the deeper coxa 4.

Schellenberg (1926) and Barnard (1927) have noted the presence of sternal processes in species of *Paramelita*. Schellenberg (1930) has reviewed the presence of such structures in this and other genera, and shown that they are probably respiratory in function. Both specimens of *P. barnardi* possess sternal processes. In each case a single medial process occurs on the second and third pereon segments, pairs on segments 4, 5 and 7, and two pairs on segment 6. Histological sections of coxal gills and sternal processes from the present material show that the two types of appendage are basically similar in structure. The most obvious differences are the smaller and less regular longitudinal lumina of the sternal appendages. Coxal gills also show well-developed transverse lumina, which are absent from the sternal structures. Despite these differences, a respiratory function for the sternal processes seems probable, as was suggested by Schellenberg.

The ecological significance of sternal gills is not clear. Amphipod species bearing sternal gills are known from many fresh-water habitats in South America, South Africa, Australia, Japan, Alaska, Scandinavia and northern Russia. Many of these species belong to the family Gammaridae, but those from Japan are eusirids of the genus *Paramoera*, while most of the South American representatives belong to *Hyaella* (Hyaellidae). Sternal gills occur in most of the *Hyaella* species found in Lake Titicaca (Dr R. J. Lincoln, personal communication). In some cases the incidence of sternal gills can be correlated with adverse ecological conditions during part of the year (e.g. Barnard 1927), but it seems unlikely that this is the case with the whole of the *Hyaella*-complex in Lake Titicaca where speciation has allowed the occupation of a wide variety of niches.

The discovery of *P. barnardi* in the dark zone of a cave, the unpigmented eyes of all species except *P. nigroculus* and the ecological data given by Barnard (1927) suggest that some members of the genus are partially troglobitic or phreatic in habit. The elongate appendages and loss of ocular elements in *Niphargus* suggest that *Paramelita* has not yet attained the obligatory subterranean status of the palaearctic genus.

SUMMARY

A new species of *Paramelita* is described from material collected in the hypogean zone of a cave on the Cape Peninsula. Evidence is presented favouring the theory of a respiratory function for the sternal processes found in this genus.

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MICHAEL H. THURSTON

A NEW SPECIES OF *PARAMELITA*
(CRUSTACEA: AMPHIPODA)
FROM SOUTH AFRICA

VOLUME 62 PART 6

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THE AMPHIPODA OF SOUTHERN AFRICA
PART 2
THE GAMMARIDEA AND CAPRELLIDEA OF
SOUTH WEST AFRICA SOUTH OF 20°S

By
C. L. GRIFFITHS

Cape Town Kaapstad

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C. L. GRIFFITHS

C.S.I.R. Oceanographic Research Unit, Zoology Department, University of Cape Town

(With 7 figures)

[MS. accepted 20 March 1973]

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INTRODUCTION

The present paper is the second of a series aimed at reviewing present knowledge of the gammaridean and caprellid amphipod fauna of Africa south of 20°S. The first of the series (Griffiths 1973) dealt with the coast of Moçambique below 20°S and recognized 65 species, 3 of them new to science and over 30 new to Moçambique. South West Africa has been chosen as the second area for analysis since its fauna makes an interesting comparison with that of Moçambique, particularly because collecting effort in the two areas has been comparable.

The marine environment of South West Africa is considerably colder than that of Moçambique, the dominant water current being the northerly flowing Benguela current, in contrast with the warm Moçambique current which bathes the east coast. The flow of the Benguela current is most intense in summer with a flow of $\frac{1}{2}$ to 1 knot 150 km offshore between 34°S and 23°S.

At Walvis Bay temperature at 50 m varies between 17°C in summer and 10°C in winter. Off Moçambique the main body of the southward flowing current passes some 90 to 120 km offshore at a surface velocity of about 3 knots (the velocity falling rapidly with depth). Inshore counter-currents often form, their intensities varying with local wind conditions. Temperature at 50 m varies from 24 to 27°C.

The first record of an amphipod from South West Africa appears to have been one of a species of *Podocerus* by Schultze (1907). These animals were about 2 mm long with transverse brown bands across their backs and were found living in small upright tubes attached to firm objects in mud and projecting about 4 mm above the surface. This species has not yet been identified or described.

Since this early record little work has been done on the Amphipoda of the area. A few records are to be found in the works of K. H. Barnard and in J. L. Barnard (1961) while more detailed surveys have been conducted by Schellenberg (1925, 1953) and Penrith & Kensley (1970).

In 1925 Schellenberg recorded 17 species from South West Africa to which 11 further species were added in 1953, 5 of them new to science. A time of inactivity followed Schellenberg's work and it was not until 1970 that Penrith & Kensley, while undertaking a survey of rocky shores in the vicinity of Lüderitz, recorded 28 species of amphipod, 15 of them new to the area; a striking demonstration of the work still to be done.

The University of Cape Town Ecological Survey has been collecting in South West Africa since 1946, particularly between 1956 and 1964. In the following account records resulting from these collections are incorporated with those of earlier workers in listing the fauna of the area. The University's collections are coded according to area and the various areas are discussed separately below: the stations are shown on Figures 1 and 2.

THE COLLECTING STATIONS

South West Africa dredge stations (SWD)

The series of samples referred to by this code consists of 95 grabs and dredges taken by the Division of Sea Fisheries research vessel *Sardinops*, the R.V. *Rockeater* and the University of Cape Town's vessel the R.V. *Gilchrist*. Thirty-four of the 95 samples contained amphipods with a total of 37 species being recorded. The general pattern of distribution indicates a number of locally abundant species, well differentiated into soft and hard substrate types, plus a larger number of relatively rare but well distributed species.

Most of the samples from soft substrates were dominated by a single species, but different species dominated closely adjoining samples. The number of amphipods in a 0.2 m² grab often exceeded 400 individuals of the dominant species, while the total population per m² was frequently in excess of 1 000. This patchy distribution is well exemplified by the two common ampelisids of the area, *Ampelisca brevicornis* and *A. palmata*. Although each dominated most of the samples in which it was found, and both occurred in close proximity to each other, they were seldom recovered from the same sample. Each of the species probably prefers a particular substrate type although unfortunately insufficient data has been collected to confirm this.

Apart from the species of *Ampelisca* mentioned, the common species of mud

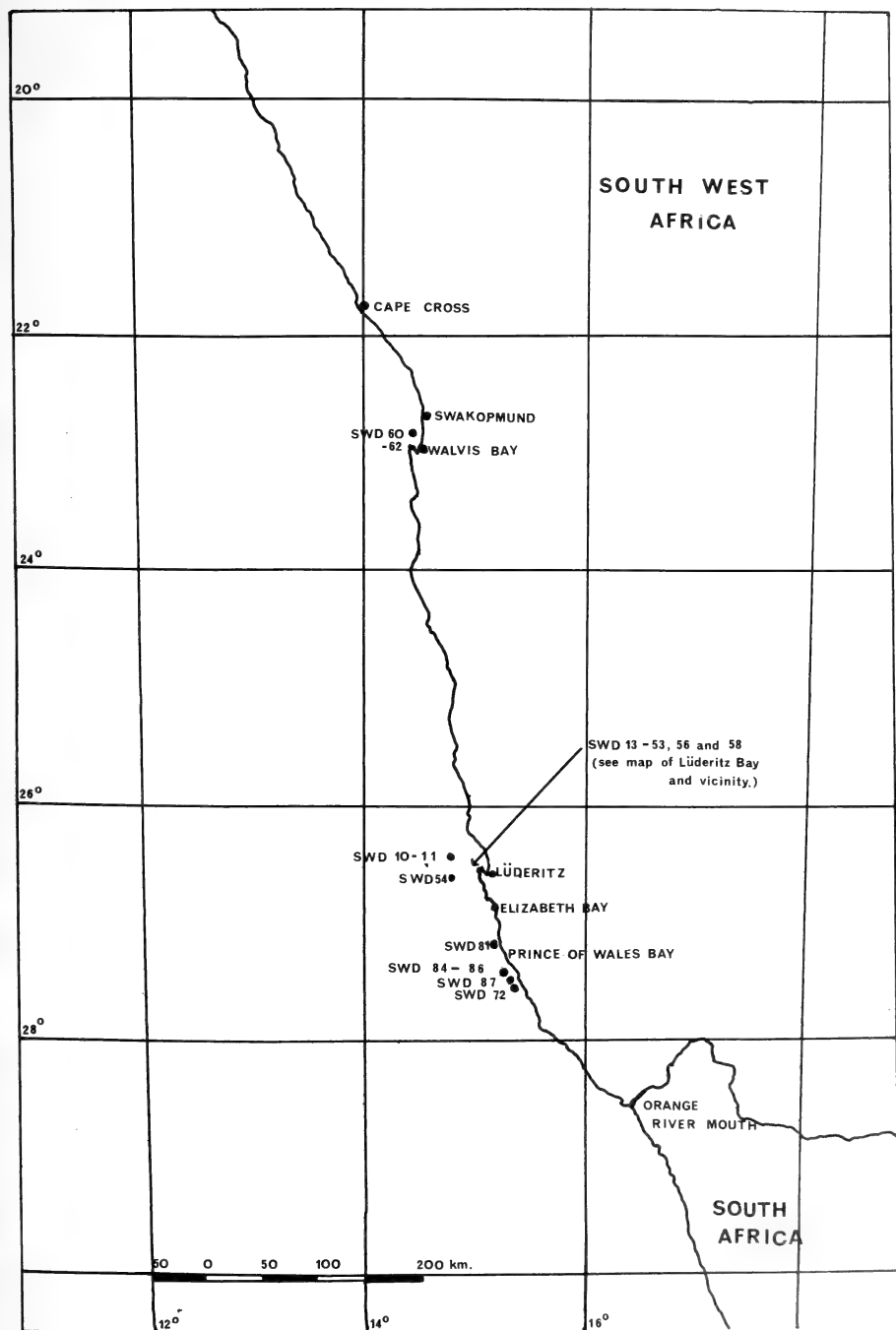


Fig. 1. South West Africa south of 20°S showing the positions of collecting stations mentioned in the text.

and sandy-mud off South West Africa were *Eriopisa epistomata* n. sp, *Perioculodes longimanus*, *Photis longidactylus* n. sp, *Photis longimanus* and *Megaluropus namaquaeensis*. *Paramoera capensis* was also common but it is found on the bottom and in the plankton in all areas, whether hard or soft bottomed.

The total population density in rocky areas was generally lower than that of mud and sand (where shelter and food are more abundant). However, occasional areas of high population density were found, especially where sponges and bryozoa covered the rocks. *Laetmatophilus purus* and *Caprella equilibra* were the most common species found in rocky areas.

South West Africa dredge station data

Catalogue no.	G = grab Date	D = dredge Position	A = airlift pump Depth (m)	Substrate	Gear	Temp. °C.
SWD 10	10/6/63	26°34'S/14°55'E	128	Mud and rock	D	11,6
SWD 11	10/6/63	26°34'S/14°55'E	128	Mud and gravel	G	11,6
SWD 13	10/6/63	26°35'S/15°01'E	71	Rock	D	12,1
SWD 16	10/6/63	26°36'S/15°06'E	26	Sandy mud	D	12,2
SWD 18	10/6/63	26°36'S/15°06'E	26	Sandy mud and shells	G	12,2
SWD 21	11/2/63	26°37'S/15°04'E	35	Rock and shells	D	11,6
SWD 24	11/2/63	26°38'S/15°06'E	11	Mud and shells	D	11,6
SWD 26	11/2/63	26°38'S/15°06'E	11	Mud and shells	D	11,6
SWD 27	11/2/63	26°38'S/15°06'E	11	Mud and shells	G	11,6
SWD 30	13/2/63	26°38'S/15°08'E	6	Grey mud	G	13,6
SWD 33	13/2/63	26°38'S/15°08'E	6	Grey mud	G	13,6
SWD 36	11/2/63	26°38'S/15°08'E	9	Dark mud	D	13,4
SWD 37	11/2/63	26°38'S/15°08'E	9	Dark mud	G	13,4
SWD 39	12/2/63	26°37'S/15°04'E	40	Rock	G	11,9
SWD 40	12/2/63	26°36'S/15°06'E	35	Fine sand	D	11,9
SWD 41	13/2/63	26°36'S/15°06'E	35	Fine sand, shells	G	11,9
SWD 44	13/2/63	26°36'S/15°10'E	5	Mud and sand	G	12,7
SWD 45	13/2/63	26°36'S/15°10'E	5	Mud and sand	G	12,7
SWD 46	13/2/63	26°25'S/15°09'E	7	Mud and sand	G	12,9
SWD 47	13/2/63	26°25'S/15°09'E	7	Mud and sand	G	12,9
SWD 48	13/2/63	26°37'S/15°10'E	6,5	Mud and sand	G	12,8
SWD 49	13/2/63	26°37'S/15°10'E	6,5	Mud and sand	G	12,8
SWD 51	14/2/63	26°37'S/15°07'E	20	Fine mud and sand	D	11,9
SWD 54	14/2/63	26°40'S/14°50'E	91	Rock	D	11,9
SWD 56	14/2/63	26°37'S/15°07'E	20	Muddy sand	G	11,9
SWD 58	14/2/63	26°39'S/15°02'E	73	Mud and gravel	D	11,9
SWD 60	9/9/63	22°53'S/14°27'E	7,6	Dark mud	G	—
SWD 61	9/9/63	22°53'S/14°27'E	14	—	G	—
SWD 62	9/9/63	22°53'S/14°27'E	14	Black mud	G	—
SWD 72	—/6/64	27°37'S/15°28'E	23	Rock	A	—
SWD 81	22/7/64	27°13'S/15°15'E	32	Rock	A	—
SWD 84	21/6/64	27°30'S/15°25'E	24	Gravel, rock	A	—
SWD 86	20/6/64	37°30'S/15°25'E	35	Gravel, stone	A	—
SWD 88	20/9/64	27°31'S/15°26'E	35	—	A	—

Lüderitz shore (LU)

One hundred and twenty-two shore samples have been taken by the University of Cape Town in the Lüderitz area and are denoted by the code LU.

Lüderitz Bay (Fig. 2) is situated on the coast of South West Africa at

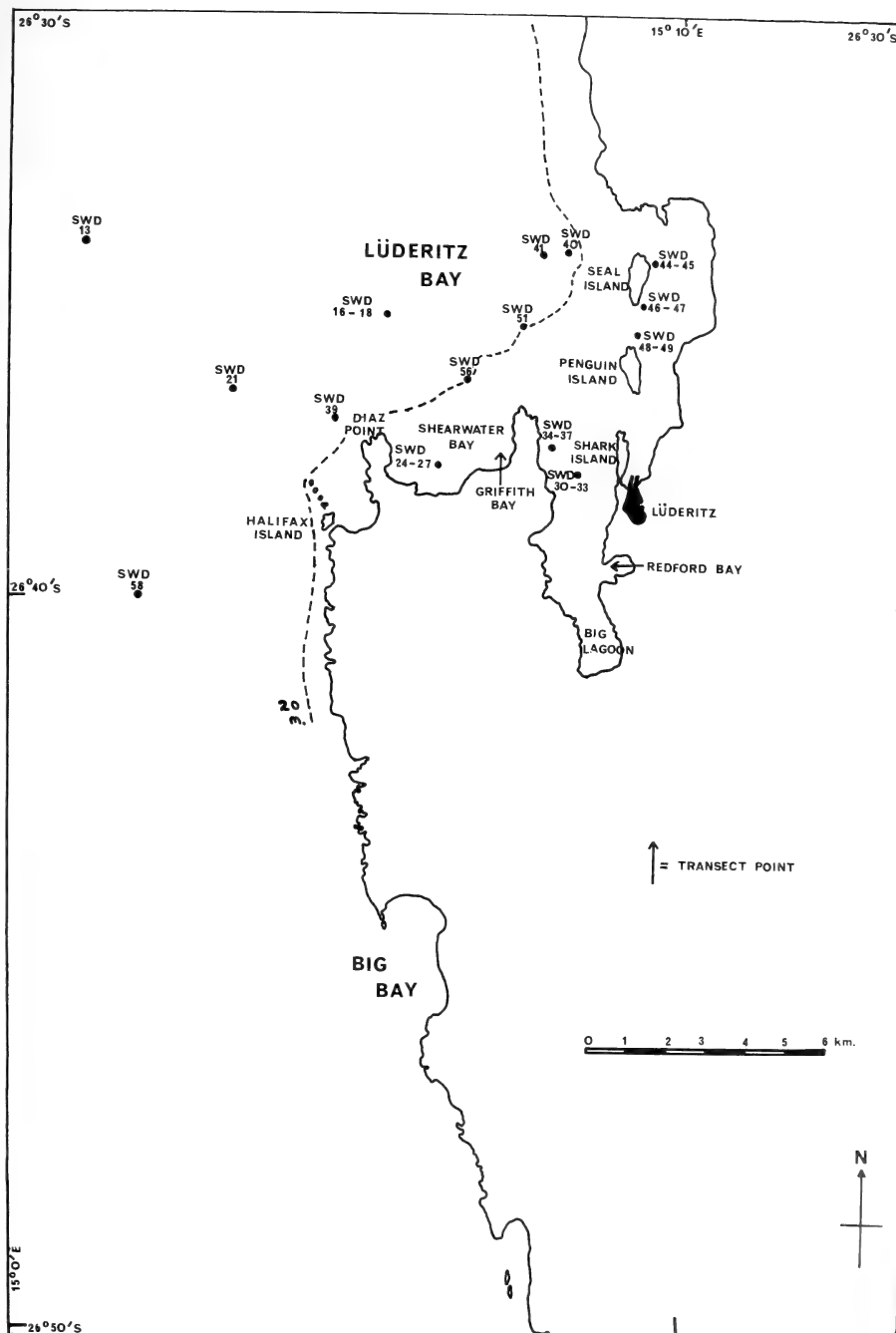


Fig. 2. Collecting stations in the Lüderitz Bay area.

26°36'S/15°08'E. The main bay is divided into a number of subsidiary bays and contains three rocky islands, Seal Island, Penguin Island and Shark Island. The shore north of the town is either sandy or rocky while the sheltered southern arm of the bay is lined with rock interspersed with considerable areas of mud, particularly to the south of Redford Bay. Shearwater Bay and Big Bay are sandy bays moderately sheltered from wave action by rocky headlands. The area between these two bays, and south of Big Bay, is rocky and exposed to powerful wave action.

The University of Cape Town team has collected 27 species of amphipod in this area. The fauna of muddy areas of the southern area of the bay lacked diversity, being dominated by *Ampelisca palmata*, which was extremely abundant (although this is inadequately reflected by the number of specimens collected since very small samples were taken at each station). The only other species of importance in muddy areas were *Lysianassa ceratina* and *Eriopisa epistomata* n. sp.

The intertidal sand flats of Shearwater Bay were almost completely barren of amphipods, with just a few *Talorchestia quadrispinosa* occurring along the drift line. The barren nature of the intertidal zone here can probably be attributed to the extreme heat and high rate of desiccation experienced in the area at low tide.

The most diverse fauna in the bay was that of rocky areas, where the greatest diversity of niches was available. Members of the genus *Hyale* were abundant, five species of that genus being recorded. Many other species were locally common, among them *Allorchestes inquirendus* on seaweeds and *Calliopiella michaelsoni* under limpets. Further details of amphipod records in rocky areas of Lüderitz Bay may be found in Penrith & Kensley (1970).

As well as the bottom samples mentioned above, a single plankton haul was taken at night near the town, revealing considerable numbers of *Paramoera capensis* and *Lysianassa ceratina*.

Lüderitz station data

Catalogue no.	Date	Locality
LU 8	16/7/46	—
LU 33	-/7/57	Intertidal rocks (location not recorded)
LU 34	-/7/57	Intertidal rocks (location not recorded)
LU 36	23/2/63	Redford Bay (mud transect, general sievings)
LU 41	23/2/63	Redford Bay (mud transect, general sievings)
LU 42	23/2/63	Redford Bay (mud transect, general sievings)
LU 44	23/2/63	Redford Bay (mud transect, general sievings)
LU 46	23/2/63	Redford Bay (mud transect, general sievings)
LU 52	24/2/63	Animals from seaweeds, Diaz Point
LU 53	24/2/63	General collection, Diaz Point
LU 54	24/2/63	General collection, Diaz Point
LU 55	24/2/63	Exposed rock, Diaz Point
LU 56	24/2/63	Exposed rock, Diaz Point
LU 57	24/2/63	Exposed rock, Diaz Point
LU 58	24/2/63	Exposed rock, Diaz Point
LU 61	25/2/63	Lüderitz township, general collection
LU 64	25/2/63	Shearwater Bay sand transect

Catalogue no.	Date	Locality
LU 66	25/2/63	Shearwater Bay sand transect
LU 76	26/2/63	End of Big lagoon, general digging
LU 78	11/2/63	Redford Bay, general mud collection
LU 81	26/2/63	End of Big Lagoon, general collection from muddy rocks
LU 82	26/2/63	End of Big Lagoon, general collection from muddy rocks
LU 86	11/2/63	Diaz Point, general collection, rocks
LU 94	21/2/63	Redford Bay, under muddy stones
LU 97	22/2/63	Shark Island, west side
LU 98	22/2/63	Shark Island, west side
LU 99	22/2/63	Shark Island, west side
LU 101	22/2/63	Shark Island, west side
LU 103	22/2/63	Shark Island, west side
LU 104	22/2/63	Shark Island, west side
LU 105	22/2/63	Shark Island, west side
LU 106	22/2/63	Shark Island, west side
LU 107	22/2/63	Shark Island, west side
LU 108	22/2/63	Shark Island, west side
LU 112	22/2/63	Shark Island, west side, bases of <i>Laminaria</i>
LU 113	22/2/63	Shark Island, west side, bases of <i>Champia</i>
LU 114	22/2/63	Shark Island, west side
LU 121	22/2/63	Plankton haul, Lüderitz township, 11 p.m.

'Africana' dredges (AFR)

Material collected by vessels of the Division of Sea Fisheries, notably the R.S. *Africana II*, and donated to the University of Cape Town, is denoted by the symbol AFR. Few of these samples fall within the region considered here, and only two of these include amphipods. Three species were recovered from these samples; *Paramoera capensis* and *Atylus guttatus* from 7 m, and *Lemboidea crenatipalma* from 60 m depth.

Africana station data

Catalogue no.	Date	Vessel	Locality	Depth Substrate
AFR 1278	9/11/48	<i>Palinurus</i>	26°07'S/14°58'E	7 m Sand and mud
AFR 1335	13/11/48	<i>Africana</i>	25°51'S/14°50'E	60 m Green mud

South West Africa shore (SWA)

This symbol denotes material collected from the South West African shore other than the Lüderitz area. Amphipoda were collected at only three SWA stations, five species being recovered, none of them common.

South West Africa shore station data

Catalogue no.	Date	Location
SWA 1	-/7/57	Swakopmund—general collection
SWA 2	-/7/57	Elizabeth Bay—general collection
SWA 4	12/7/57	Cape Cross shore—general collection

Orange River mouth (OR)

This material was collected when the University of Cape Town Ecological Survey Team, under Professor A. C. Brown, visited the Orange River mouth in 1956. The results of this survey have been published in detail by Brown (1959).

The Orange River estuary was found to be faunistically barren, indeed no true estuarine species of any group was found. This paucity can be attributed to the fact that during the wet season fresh-water flow extends throughout the system and estuarine conditions cease to exist. Those animals which were recovered represented either true fresh-water types (found in the upper reaches), or true marine types (from the sea shore). The only amphipod found, *Talorchestia quadrispinosa*, occurred above the drift line on the beach and amongst the sand dunes surrounding the river mouth.

Orange River station data

<i>Catalogue no.</i>	<i>Date</i>	<i>Location</i>
OR 2	7/7/56	Above H.W.S. at mouth of estuary

SYSTEMATICS

In the following account families and genera are presented in alphabetical order. No attempt has been made to provide a full list of synonyms or references for each species, but reference is given to one or more of the better and more readily available descriptions. Preference has been given to descriptions which incorporate good figures, or which refer specifically to the southern African region. Brief diagnostic descriptions are given for those species not described in Part I of this series. The diagnoses are intended to differentiate the species in question from others of the same genus, or in the largest genera (e.g. *Ampelisca*) from those members of the genus found in the southern African area.

Diagnoses of Gammaridean families and genera, and keys to generic level, may be found in J. L. Barnard (1969b, 1970). References to all known caprellid species and species lists for various areas are found in McCain & Steinberg (1970). Taxonomy within the Caprellidea follows McCain (1970). The type material of all new species has been placed in the South African Museum, Cape Town.

The limbs of the pereon are referred to throughout as gnathopods 1 and 2, followed by pereiopods 1 to 5 (as in K. H. Barnard and J. L. Barnard). It should be noted that authors such as McCain, Schellenberg and Ledoyer number pereiopods according to the pereon segments on which they occur, i.e. gnathopods 1 and 2 followed by pereiopods 3 to 7. The articles of a limb are numbered from 1 to 7, the coxal plate (whether present or absent) being the first article. Numbers in brackets following each catalogue number refer to the number of individuals in that sample. Material from depths of over 1 000 m is not considered to form a part of the continental fauna and has thus been excluded.

Suborder GAMMARIDEA

Family **Ampeliscidae***Ampelisca brachyceras* Walker, 1904

Ampelisca brachyceras Walker, 1904: 252, pl. 2, fig. 13.

Records: SWD 21F (1).

Diagnosis: Antennae subequal, less than $\frac{1}{2}$ body length, antenna 2 originating immediately below 1; gnathopod 1 normal; article 5 of pereopods 3 and 4 produced postero-distally for $\frac{3}{4}$ length of article 6; article 3 of pereopod 5 longer than article 4, article 4 not lobed posteriorly; hind margin of third pleonal epimeron convex, lower corner upturned.

Distribution: Ceylon, southern Africa.

Ampelisca brevicornis (Costa, 1853)

Ampelisca brevicornis: Ledoyer, 1967: 123, fig. 2. Reid, 1951: 204-210, figs 9-15.

Records: SWD 44J (10), SWD 46J (9), SWD 47N (33), SWD 48R (3), SWD 49Q (47); Lüderitz (Schellenberg 1925, Penrith & Kensley 1970).

Diagnosis: Antenna 1 shorter than peduncle of 2, antenna 2 half body length, its origin well separated from that of antenna 1; gnathopod 1 normal; article 5 of pereopods 3 and 4 not produced posteriorly-distally; article 3 of pereopod 5 slightly shorter than article 4, article 4 lobed postero-distally to completely overlap triangular article 5; hind margin of third pleonal epimeron deeply bisinuate, lower corner with a large upturned tooth.

Distribution: Cosmopolitan.

Ampelisca fusca Stebbing, 1888

Ampelisca fusca Stebbing, 1888: 1052, 1651, pl. 105.

Records: SWD 84W (6), SWD 88E (1), SWD 86B (common).

Distribution: Moçambique to South West Africa.

Remarks: The present specimens are much larger (12 mm excluding antennae) than those from the east coast and differ from them in having a distinct red pigment spot behind the upper pair of eyes and short plumose setae on the inside of article 2 or pereopod 5.

Ampelisca palmata K. H. Barnard, 1916

Ampelisca palmata K. H. Barnard, 1916: 136, pl. 28, figs 30-31.

Records: SWD 16K (17), SWD 18C (8), SWD 21G (14), SWD 26G (11), SWD 27M (11), SWD 33E (448), SWD 36C (116), SWD 37K (188), SWD 40L (5), SWD 41H (7), SWD 44G (1), SWD 45F (1), SWD 48P (2), SWD 51H (6), SWD 60C (32), SWD 61C (159), SWD 62C (55); LU 46B (21), LU 78E (8), LU 121J (1).

Distribution: Senegal to Moçambique.

Remarks: This species is more variable than indicated by Barnard's description, in particular the antennae may be considerably shorter than in the type specimens. This has led to confusion between this species and *Ampelisca spinimana* but the two can be readily distinguished by the presence of a produced lobe on the anterior margin of article 4 of pereopod 5 in *A. palmata*.

Ampelisca spinimana Chevreux, 1887

Ampelisca spinimana: Chevreux & Fage, 1925: 81, fig. 73.

Ampelisca spinimana f. aspinosa Schellenberg, 1925: 127.

Records: Lüderitz (Schellenberg 1925).

Diagnosis: Antenna 1 slightly exceeding peduncle of 2; antenna 2 less than $\frac{1}{3}$ body length, its origin well separated from that of antenna 1; palm of gnathopod 1 spinose (variable); article 5 of pereopods 3 and 4 not produced postero-distally; article 3 of pereopod 5 longer than article 4, article 4 not lobed anteriorly or posteriorly; hind margin of third pleonal epimeron straight, lower corner quadrate.

Distribution: Eastern Atlantic.

Family **Amphilochidae**

Cyproidea ornata Haswell, 1880

Cyproidea ornata: Schellenberg, 1953: 113, fig. 2. Ledoyer, 1967: 125, fig. 4a.

Records: Lüderitz, Walvis Bay (Schellenberg 1953).

Diagnosis: Article 3 of gnathopod 2 postero-distally produced into an acute lobe, terminating in two large spines; article 6 not expanded distally, palm smooth.

Distribution: Indo-Pacific, extending to South West Africa.

Gitanopsis pusilla K. H. Barnard, 1916

Gitanopsis pusilla K. H. Barnard, 1916: 144.

Records: Swakopmund, Lüderitz (Schellenberg 1925); Lüderitz (Penrith & Kensley 1970).

Distribution: Moçambique to South West Africa.

Hoplopleon medusarum K. H. Barnard, 1932

Hoplopleon medusarum K. H. Barnard, 1932: 105, fig. 54.

Records: Lüderitz (Penrith & Kensley 1970).

Diagnosis: Hind margin of article 2 of pereopods 4 and 5 straight; dactyl of gnathopod 2 simple; palm of gnathopod 2 transverse, concave, defining angle rounded, bearing four strong spines.

Distribution: Endemic, Saldanha Bay to Lüderitz.

Hoplopleon similis Schellenberg, 1953

Hoplopleon similis Schellenberg 1953: 113, fig. 2.

Records: Lüderitz (Schellenberg 1953).

Diagnosis: Hind margin of article 2 of pereopods 4 and 5 straight; dactyl of gnathopod 2 cut into two teeth; palm of gnathopod 2 transverse, concave, defined by a single very large spine.

Distribution: Endemic, known only from the above record.

Family **Ampithoidae***Ampithoe falsa* K. H. Barnard, 1932

Ampithoe brevipes: K. H. Barnard, 1916: 255, pl. 28, fig. 34.

Ampithoe falsa: Ruffo, 1969: 57, figs 18–20.

Records: Lüderitz (Penrith & Kensley 1970).

Diagnosis: Article 2 of gnathopod 2 not lobed; article 6 of gnathopod 1 rectangular, palm transverse; palm of gnathopod 2 concave but otherwise not distinct from hind margin, a small rectangular tooth at the finger hinge; article 2 of pereopods 1 and 2 ovate, strongly expanded.

Distribution: Gulf of Aden, Arabian Sea, India, southern Africa.

Ampithoe ramondi (Audouin, 1826)

Ampithoe vaillanti: K. H. Barnard, 1916: 253.

Ampithoe ramondi: Ledoyer, 1967: 135, fig. 24.

Records: LU 61Z (1), LU 112S (2); Lüderitz (Penrith & Kensley 1970).

Distribution: Cosmopolitan in warm and temperate seas.

Family **Aoridae***Aora typica* Kröyer, 1845

Aora typica: Ledoyer, 1967: 131, fig. 15.

Records: LU 112V (2); SWD 51N (1); Lüderitz (Schellenberg 1953, Penrith & Kensley 1970).

Distribution: Cosmopolitan.

Lemboides afer Stebbing, 1895

Lemboides afer: K. H. Barnard, 1932: 222, fig. 137.

Records: SWD 26J (2).

Diagnosis: Pereon of ♂ with ventral processes on segments 2–6; gnathopod 1 ♂ palm transverse, a broad denticulate cavity between a strong tooth near finger hinge and two smaller teeth at defining angle, dactyl hardly exceeding palm;

gnathopod 2 palm concave, defined by a large stout spine, dactyl slightly longer than palm, denticulate.

Distribution: Endemic, False Bay to South West Africa.

Lemboides crenatipalma K. H. Barnard, 1916

Lemboides crenatipalma K. H. Barnard, 1916: 240, pl. 28, figs 9–10.

Records: SWD 13T (4), SWD 21M (2), SWD 58B (8); AFR 1335 (present).

Diagnosis: Pereon of ♂ without ventral processes; gnathopod 1 ♂, palm transverse, crenulate, defined by a blunt lobe-like projection; dactyl overlapping palm; gnathopod 2 palm concave, defined by a long, stout, subacute tooth with a short spine at its base; dactyl longer than palm, denticulate.

Distribution: Endemic, Saldanha Bay to South West Africa.

Lembos hypacanthus K. H. Barnard, 1916

Lembos hypacanthus K. H. Barnard, 1916: 237, pl. 28, figs 5–6.

Records: SWD 60B (3), SWD 61B (8), SWD 62B (9); Swakopmund (Schellenberg 1925).

Diagnosis: Male pereon segments 3–7 with strong medio-ventral spines; article 6 of gnathopod 1 ♂ equal to article 5, palm slightly oblique, a small tooth near the finger hinge and a spiniform process and stout spine at the defining angle, finger serrate, longer than palm; gnathopod 2 ♂ with distal apex of article 2 produced into a recurved hook.

Distribution: Endemic, Natal to South West Africa.

Lembos teleporus K. H. Barnard, 1955

Lembos teleporus K. H. Barnard, 1955: 94, fig. 47. Ledoyer, 1967: 133, figs 16–17.

Records: SWD 13U (4), SWD 21P (4).

Distribution: Southern Africa, Madagascar.

Family **Calliopiidae**

Calliopiella michaelsoni Schellenberg, 1925

Calliopiella michaelsoni Schellenberg, 1925: 147. K. H. Barnard, 1940: 451, fig. 24.

Records: LU 33H (1), LU 81P (2), LU 96C (1), LU 108A (1); SWA 2T (1); Swakopmund (Schellenberg 1925); Lüderitz (Penrith & Kensley 1970).

Diagnosis: Found under limpets, where it is common. Article 6 of gnathopod 2 twice as long as broad, palm oblique, defined by 2–5 large spines, dactyl cut into 5 teeth, a setule in each notch; uropod 3 with rami equal to peduncle, spination variable; telson varying from cleft to rounded with age.

Distribution: Endemic, False Bay to South West Africa.

Remarks: Extensive sampling throughout the range of this species has shown it to be much more variable than was previously thought. Colour varies with the species of *Patella* under which the animal lives and there seems to be a preference for particular hosts. For example, 90% of *Patella compressa* shelter *Calliopiella* of a bright pink to plum colour, whereas 50% of *Patella tabularis* reveal pale blue specimens with bright red dorsal stripes. Less favoured species are *Patella barbara* (5%, pale brown), *P. cochlear* (5%, pale brown to green), *P. argenvillei* (10%, whitish with green gut), and *P. granularis* (20%, pale brown to green). Other species of *Patella* show an intermediate percentage of amphipods.

In all species of *Patella* there is a size relationship between the host and amphipod, specimens of *Calliopiella* being as large as 17 mm in the largest *Patella compressa*. The amphipods are almost always found in pairs, the male and female being of similar size.

A number of morphological changes with age have been noted, for example, in the smallest specimens (4 mm) the telson is up to 40% cleft, a continuous range being found through notched and emarginate, to smoothly rounded in the largest specimens (17 mm). The uropods are also extremely variable, uropod 3 ranging from pointed to rounded and showing a variable number of spines on its inner surface. Terminal setae may or may not be present.

The number of defining spines on gnathopod 2 varies between 2 and 5. These morphological changes appear to vary solely with size and are independent of the species of *Patella* occupied.

Metaleptamphopus membrisetata J. L. Barnard, 1961

Metaleptamphopus membrisetata J. L. Barnard, 1961: 105, fig. 73.

Records: 20°04'S/11°56'E, 537 m (J. L. Barnard 1961).

Diagnosis: Antenna 1 longer than antenna 2, accessory flagellum uniarticulate; upper lip rounded below, not incised; gnathopods subchelate, not greatly elongate, article 5 slightly shorter than 6; article 7 of pereopods 1-5 bearing anterior pectinations in the form of short spines; rami of uropod 3 subequal to the elongate peduncle, spinose, outer slightly the shorter; telson apically rounded, smooth.

Distribution: The above record is the only one to date.

Family **Corophiidae**

Corophium acherusicum Costa, 1857

Corophium acherusicum: Sivaprakasam, 1970b: 156, fig. 14.

Records: Lüderitz (Penrith & Kensley 1970).

Diagnosis: Article 4 of antenna 2 ♂ distally produced into a large curved tooth with a smaller tooth on its inner edge; rostrum obsolete, head deeply invagi-

nated in dorsal view; article 7 of gnathopod 2 tridentate; pleon segments coalesced.

Distribution: Cosmopolitan in tropical and temperate seas.

Grandidierella chelata K. H. Barnard, 1951

Grandidierella chelata K. H. Barnard, 1951: 708, fig. 7.

Records: SWD 13S (2).

Diagnosis: Body without ventral spines; coxae 1 and 2 semicircular, very shallow, not pointed; gnathopod 1 ♂ with article 5 ovoid, lower margin with a strong spiniform projection proximally and a stout tooth distally, the teeth becoming further apart with growth; gnathopod 1 ♀ with article 5 ovate and article 6 with four strong spines on its lower margin.

Distribution: Endemic, Natal to South West Africa. This is the first record of this species from the open sea.

Siphonoecetes dellavallei Stebbing, 1893

Siphonoecetes dellavallei: Stebbing, 1906: 684.

Records: SWD 21H (1).

Diagnosis: Rostrum acute; eyes well developed; antenna 1 scarcely extending to the tip of peduncle of antenna 2, flagellum less than half as long as peduncle, five-articulate; coxa 1 blunt anteriorly.

Distribution: Bay of Naples, southern Africa.

Family **Dexaminidae**

Atylus guttatus (Costa, 1851)

Nototropis guttatus: Chevreux & Fage, 1925: 194, figs 201–203.

Records: AFR 1278F (1).

Diagnosis: Pereon segment 7 and pleon segments 1–3 each with a single dorsal carina; urosomite 1 with two teeth separated by a marked slit; composite urosomite 2–3 with two spinose humps; pereopod 3 with article 2 moderately produced postero-distally.

Distribution: Mediterranean, Atlantic.

Atylus swammerdami (Milne-Edwards, 1830)

Atylus swammerdami: Chevreux & Fage 1925: 195, fig. 204.

Records: SWD 16N (3), SWD 21K (3), SWD 26H (3).

Diagnosis: Pereon and pleon dorsally smooth; urosomite 1 with a small dorsal tooth followed by a much larger one; composite urosomite 2–3 without spinose humps; pereopod 3 with article 2 moderately produced.

Distribution: Mediterranean, Atlantic (including south coast of South Africa).

Guernea (Guernea) rhomba n. sp.

Fig. 3

Guernea laevis: K. H. Barnard, 1916: 213-215.*Guernea coalita laevis*: Schellenberg, 1953: 118-119 (Lüderitz).*Guernea laevis*: Penrith & Kensley 1970: 230 (Lüderitz).

Description of female (3 mm): Head slightly longer than two pereon segments; eyes composed of regularly sized, closely compacted ommatidia; article 1 of antenna 1 lacking a dorsal notch, longer than articles 2 plus 3, flagellum 4-articulate, accessory flagellum not visible; article 4 of antenna 2 lobed ventrally, distally finely setose, flagellum 3-articulate; palp of maxilla 1 extending to tip of outer lobe, terminating in five setae; inner plate of maxilla 2 tipped by seven strong setae, outer plate longer than inner, apex rounded, six long setae terminally and another on the outer margin.

Coxa 1 60% as long as coxa 2; apex subacute, rounded; articles 5 and 6 of gnathopod 1 subequal, article 5 with a group of strong setae postero-inferiorly, palm defined by three strong spines; article 2 of gnathopod 2 widening from its origin, articles 5 and 6 longer than those of gnathopod 1, palm straight, transverse, defined by four strong spines, a row of small spines along inner margin of palm; article 5 of pereopod 1 with six strong spines along its posterior margin, article 6 with four spines; pereopod 2 with three strong terminal spines on article 5 and four posterior and two lateral spines on article 6; article 2 of pereopod 3 rhomboidal, anterior margin convex, posterior margin extended into a subacute process, anterior margin naked, article 4 with a single plumose seta antero-distally and another postero-distally, articles 5 and 6 terminating in small spines; article 2 of pereopod 4 evenly rounded posteriorly, article 4 with a few plumose setae anteriorly, article 5 with two posterior and two terminal spines; article 2 of pereopod 5 quadrate, article 4 and 5 with plumose setae on both posterior and anterior margins, article 6 unarmed.

Pleonal epimera postero-inferiorly rounded; urosomite 1 slightly concave dorsally, urosomites 2 and 3 fused, not notched, not spinose, evenly rounded posteriorly; uropod 1 with outer ramus slightly longer than inner, terminating in two lateral spines and a medial spine which is less than 25% the length of the ramus (fig. 3F); uropod 2 similar to 1 but shorter; uropod 3 broader than 1 and 2, rami unarmed.

Cuticular ornamentation moderate, fairly strong polygons visible on article 2 of pereopods.

Colour (in life): Yellowish, pereon segments 6 and 7 and pleon segment 1 bright orange.

Holotype: SAM A2936, female, 3 mm.

Type-locality: Sea Point, near Cape Town, 26 February 1914. This specimen, rather than one from South West Africa, has been chosen as the holotype as it is the one erroneously described by K. H. Barnard as *G. laevis*.

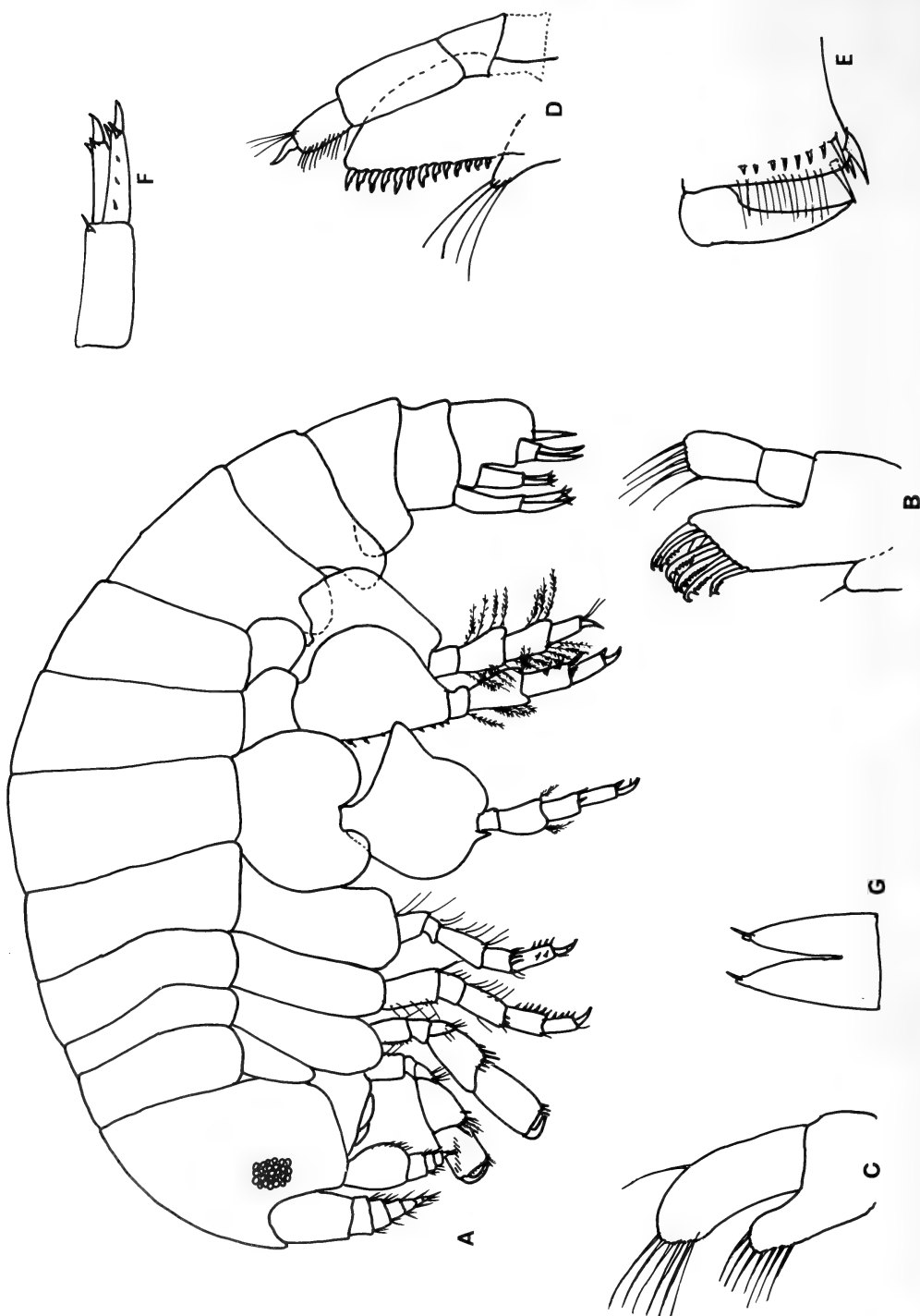


Fig. 3. *Guerneia (Guerneia) rhomba* n. sp., holotype, female, 3 mm.
A. Lateral aspect. B. Maxilla 1. C. Maxilla 2. D. Maxilliped. E. Palm of gnathopod 2. F. Uropod 1. G. Telson.

Remarks: These specimens, although they lie close to *Guernea coalita* (Norman), differ from that species in the following respects:

Urosomite 2 plus 3 is not dorsally notched; article 4 of antenna 2 is lobed; the inner lobe of maxilla 2 has seven rather than two setae; article 2 of pereopod 3 lacks anterior setae and has a pronounced posterior semiacute process; the spines on uropods 1 and 2 are much shorter.

The short spines on the uropods of this species also distinguish it from other members of the subgenus *Guernea*.

Species of the subgenus *Prinassus* are distinguished by a retrose dorsal process on the urosome of the female and a high dorsal keel in the male.

Distribution: Lüderitz to Cape Town.

Polycheria atolli Walker, 1905

Polycheria antarctica: K. H. Barnard, 1916: 211.

Polycheria atolli: Ledoyer, 1967: 131, fig. 13a.

Records: Lüderitz (Schellenberg 1925).

Distribution: Antarctic and southern oceans, tropical Indian Ocean.

Family **Eusiridae**

Paramoera bidentata K. H. Barnard, 1932

Paramoera bidentata K. H. Barnard, 1932: 211, figs 118 m, 129.

Records: Lüderitz (Penrith & Kensley 1970).

Diagnosis: Rostrum small, acute; post-antennal angle of head acutely produced; eyes nearly meeting on top of the head; pleon segments 1 and 2 postero-dorsally produced into subacute triangular teeth; third pleonal epimeron quadrate with a small postero-inferior point; urosomite 1 with a dorsal transverse depression medially; apices of telson acute, with 2 unequal spiniferous notches.

Distribution: Endemic, Still Bay to South West Africa.

Paramoera capensis (Dana, 1853)

Paramoera capensis: K. H. Barnard, 1916: 183-186; 1932: 210, figs 118 m, 129.

Records: SWD 16H (18), SWD 26B (190), SWD 27K (2), SWD 30F (1), SWD 33F (2), SWD 36E (1), SWD 37N (2), SWD 41K (4), SWD 44K (70), SWD 45E (1), SWD 46K (3), SWD 47P (22), SWD 48M (65), SWD 49R (75); LU 52H (4), LU 54E (5), LU 57H (1), LU 58M (1), LU 61Z (7), LU 82Q (1), LU 99J (3), LU 101Z (2), LU 112R (21), LU 121K (53); AFR 1278E; Swakopmund, Possession Island, Lüderitz (Schellenberg 1925); Lüderitz (Penrith & Kensley 1970).

Diagnosis: Rostrum represented by a short point; post-antennal angle of head rounded-quadrate, not produced; eyes nearly meeting on top of the head; pleon

segments lacking teeth; third pleonal epimeron rounded-quadrate with a small postero-inferior point; urosomite 1 not dorsally depressed; apices of telson truncate, cut into five to eleven teeth.

Distribution: Atlantic, and Indo-Pacific.

Family **Gammaridae**

Ceradocus rubromaculatus (Stimpson, 1855)

Ceradocus rubromaculatus: Ledoyer, 1968: 39, fig. 14.

Records: SWD 81E (1); LU 54A (6); Swakopmund, Lüderitz (Schellenberg 1925); Lüderitz (Penrith & Kensley 1970).

Diagnosis: Pleon segments 1–5 postero-dorsally toothed; pleonal epimera 1–3 strongly serrate posteriorly and slightly serrate below; gnathopod 2 with article 6 large, palm oblique, defined by a large tooth and with a large flat topped tooth along its length; rami of uropod 3 large, foliate, subequal, both margins strongly serrate; telson cleft nearly to base, two spines at apex of each lobe; colour mottled or banded rose pink.

Distribution: Indo-Pacific, extending to South West Africa.

Elasmopus japonicus Stephensen, 1932

Elasmopus spinimanus (non Walker 1905): K. H. Barnard, 1925: 358.

Elasmopus japonicus: Sivaprakasam, 1968: 278, figs 3–5.

Records: LU 57H (1).

Distribution: Japan, India, southern Africa.

Eriopisa epistomata n. sp.

Fig. 4

Description of male (14 mm): Anterior margin of head concave, eyes absent; antenna 1 extending to end of body, articles 1 and 2 subequal, article 3 very short, flagellum 30–40 articulate, twice as long as peduncle, accessory flagellum of two small articles; antenna 2 less than half as long as 1, article 2 produced ventrally, articles 4 and 5 subequal, flagellum of one long and two small articles; primary cutting edge of mandible with five teeth, secondary cutting edge of four teeth, palp article 3 medially expanded and setose, subequal to article 2; inner plate of maxilla 1 heavily setose, outer plate with six spines; inner and outer plates of maxilliped with plumose setae.

Article 4 of gnathopod 1 with a posterior pellucid lobe, articles 5 and 6 subequal, palm evenly convex, dactyl equal to palm; coxa 1 strongly produced anteriorly; gnathopod 2 much larger than 1, article 5 subtriangular, article 6 oval, palm oblique, irregularly nodulose, convex near finger hinge but concave proximally, defined by two large spines; dactyl marginally longer than palm;

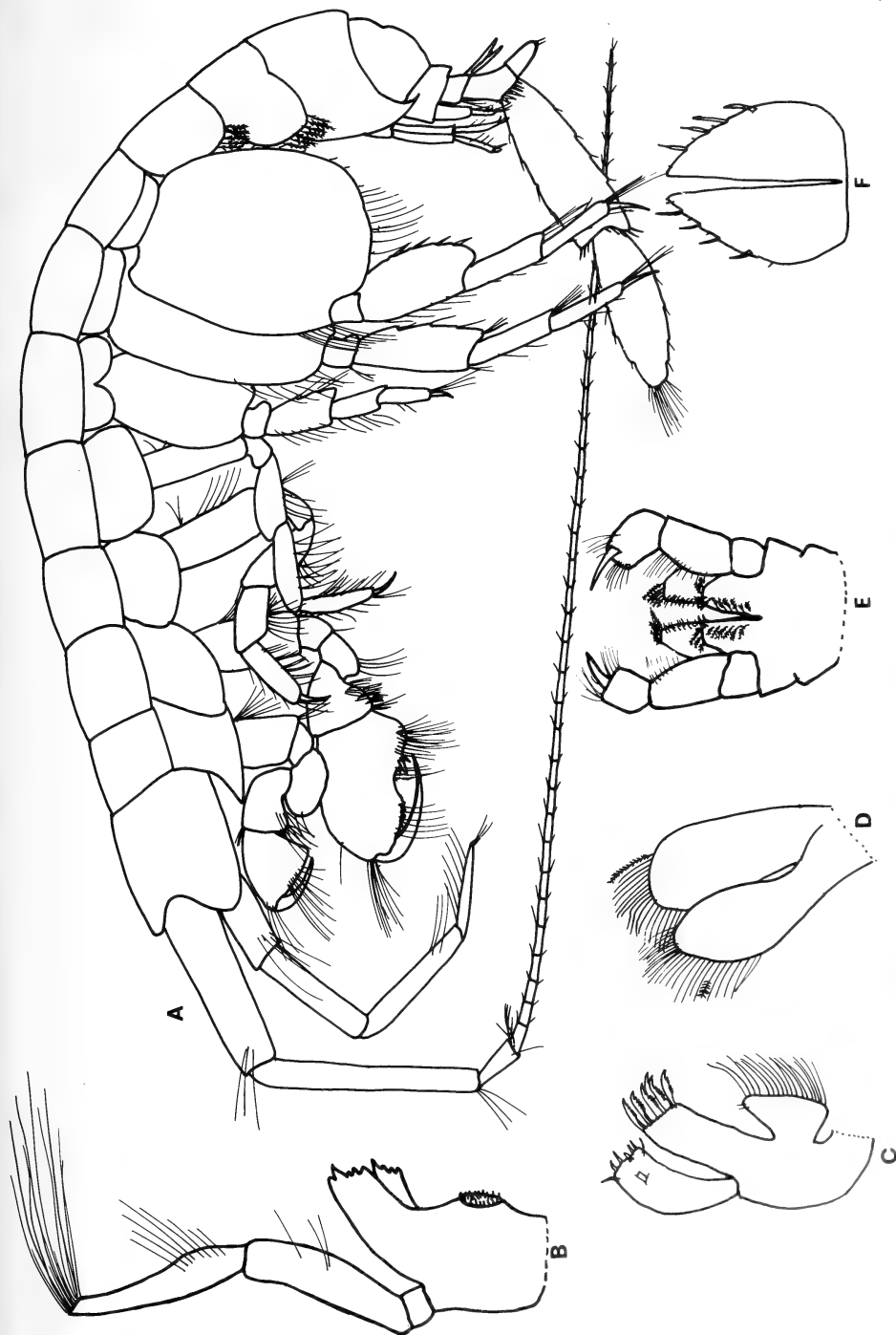


Fig. 4. *Eriopisa epistomata* n. sp., holotype, male, 1.4 mm.
A. Lateral aspect. B. Mandible. C. Maxilla 1. D. Maxilla 2. E. Maxilliped. F. Telson.

branchiae large, extending beyond the end of article 2 of gnathopods; pereopods 1–3 much smaller than 4 and 5, branchiae extending to tip of article 3; article 2 of pereopods 4 and 5 expanded, especially that of pereopod 5; article 4 of both limbs with 4 or 5 posterior serrations.

Pleonal epimera 1 and 2 rounded-quadrate, ventrally bearing a few plumose setae; third pleonal epimeron postero-distally produced into an upturned tooth; peduncle of uropod 1 quadrate in section, dorsal surface terminating in two spines, inner ramus with one dorsal and two terminal spines, outer ramus with three dorsal and two terminal spines; uropod 2 shorter than 1 but with similar spination; peduncle of uropod 3 subtriangular, inner ramus small, oval with two terminal spines; outer ramus as long as pleon and urosome together, articles 1 and 2 subequal, article 1 distally excavate and laterally slightly serrate, its distal corners spinose, article 2 with 5 serrations on each edge and a dense terminal tuft of setae; telson extending to tip of peduncle of uropod 3, cleft to base, outer margin of each lobe with four spines.

Female: Similar to male but with a smaller second gnathopod, its palm less deeply concave; antenna 1 shorter than that of male.

Holotype: SAM A13070, male, 14 mm.

Type-locality: SWD 37L, 26°38'S/15°08'E, 11 February 1963, depth 9 m, substrate dark mud.

Remarks: This species belongs to the group with an elongate article 2 to the outer ramus of uropod 3. From amongst these species the lack of eyes and produced third pleonal epimeron distinguish it from *E. chilensis* (Chilton) while the inner plate of maxilla 1 differs from that of *E. garthi* J. L. Barnard, and the anteriorly produced coxa 1 from that of *E. philippensis* Chilton. *E. elongata* (Bruzilius) can be distinguished by its lateral cephalic notch.

Material: SWD 27N (8), SWD 30B (25), SWD 33B (31), SWD 36B (13), SWD 37L (24), SWD 47Q (1), SWD 48N (1), SWD 49T (1); LU 78B (8).

Eriopisella epimera n. sp.

Fig. 5

Description of male (5 mm): Ocular lobes angularly rounded, eyes composed of about nine well spaced ocelli; article 1 of antenna 1 large, remaining segments missing; article 2 of antenna 2 ventrally produced, article 4 extending to tip of article 1 of antenna 1, flagellum 9 articulate; maxilla 2 setose only terminally; articles 2 and 3 of mandibular palp subequal, article 3 terminally with three long setae.

Coxa 1 produced forwards as far as rear of eye; coxae 1–4 each with two small setae in minute notches at antero-distal corners; article 4 of gnathopod 1 finely setose posteriorly, article 6 as long as 5, palm convex, not defined; palm of gnathopod 2 defined by a large spine and bearing six large spines along its length, each with a seta on its posterior margin; article 5 of pereopods 1 and 2

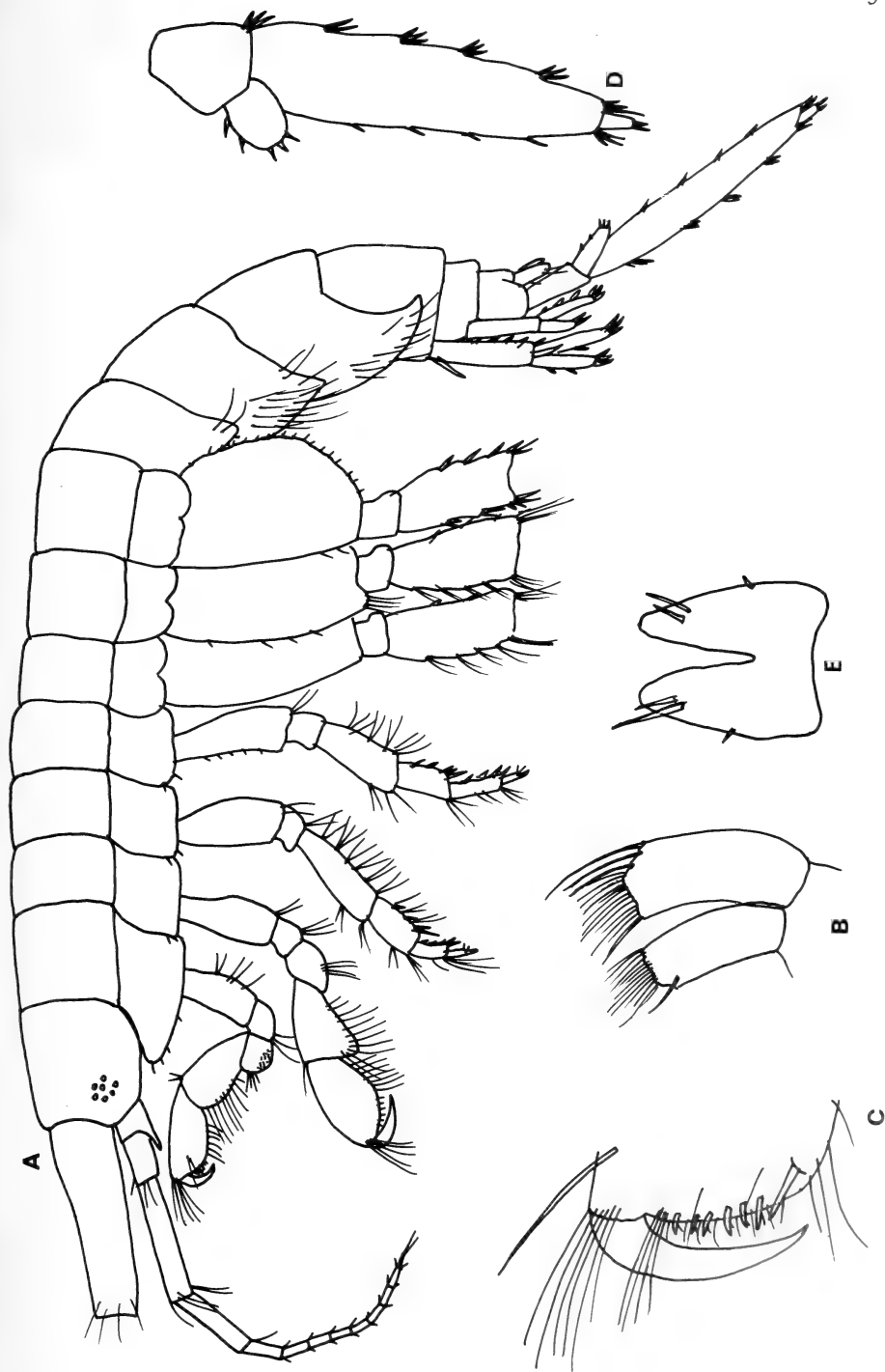


Fig. 5. *Eriopsisella epimera* n. sp., holotype, male, 5 mm.
 A. Lateral aspect. B. Maxilla 2. C. Palm of gnathopod 2. D. Uropod 3. E. Telson.

with three groups of heavy spines along posterior margins, article 6 with four groups of spines, dactyl medially constricted, bearing two accessory setae at the constriction; pereopods 3-5 with article 2 progressively wider and faintly serrate posteriorly, a short seta in each notch.

First pleonal epimeron postero-distally quadrate with two long setae on its outer surface; second pleonal epimeron with about 20 lateral setae; third pleonal epimeron broadly convex below, posteriorly produced into a large upturned tooth, scattered setae on its lower external surface; peduncle of uropod 1 with a large proximal spine on its ventral surface and another large spine at its apex; rami subequal; outer ramus of uropod 2 slightly shorter than inner; outer ramus of uropod 3 20% as long as inner ramus, with three terminal and two lateral spines, inner ramus bi-articulate, article 2 hardly 10% as long as article 1, article 1 with four lateral fascicles of spines on its inner margin, four single spines along its outer edge and a terminal group of spines which extend to the tip of article 2; telson 70% cleft, two large terminal and a small lateral spine on each lobe.

Female: Exactly like the male except for the possession of brood lamellae. Ovigerous at 4.5 mm.

Colour (as preserved): Uniform brown.

Holotype: SAM A13071, male, 5 mm.

Type-locality: SWD 13R, 26°35'/15°01'E, 10 February 1963, depth 71 m, substrate rocky.

Remarks: The present species is readily distinguishable from *Eriopisella capensis* K. H. Barnard and *E. pusilla* Chevreux by its relatively well-developed eyes and produced third pleonal epimeron. It lies closer to *E. sechellensis* Chevreux and *E. nagatai* Gurganova, but of these the former has a hirsute article 2 to pereopod 5 and a longer article 2 of uropod 3, while in the latter article 2 of pereopod 5 overhangs article 3 and articles 5 and 6 of gnathopod 2 are triangular.

Material: SWD 13R (9).

Maera grossimana (Montagu, 1808)

Maera grossimana: Chevreux & Fage, 1925: 239, figs 248, 250.

Records: Swakopmund (Schellenberg 1925).

Diagnosis: Coxa 1 acutely produced forwards; article 6 of gnathopod 2 longer than broad, palm oblique, regularly serrate (♂) or irregularly notched (♀), defined by a distinct tooth; third pleonal epimeron posteriorly smooth, postero-distally acutely produced; uropod 2 slightly exceeding 1 and 2, rami equal, truncate, terminally strongly setose.

Distribution: Mediterranean, Atlantic.

Maera hirondellei Chevreux, 1900

Maera hirondellei: Chevreux & Fage, 1925: 241, fig. 252. Reid, 1951: 239, fig. 34.

Records: Lüderitz (Penrith & Kensley 1970).

Diagnosis: Coxa 1 acutely produced forwards; article 6 of gnathopod 2 longer than broad, palm oblique, irregularly toothed but always with a larger tooth near finger hinge and an acute defining tooth; third pleonal epimeron posteriorly smooth, postero-distally slightly produced; uropod 3 considerably exceeding 1 and 2, rami subequal, rounded, terminally moderately setose.

Distribution: Eastern Atlantic, Mediterranean.

Maera inaequipes (Costa, 1851)

Maera inaequipes: J. L. Barnard, 1959: 25, pl. 5.

Records: SWD 21J (1), SWD 84Y (1); LU 86X (1), LU 99H (1), LU 112V (2), LU 114W (1); Lüderitz (Penrith & Kensley 1970).

Distribution: Cosmopolitan in tropical and temperate seas.

Maera vagans K. H. Barnard, 1940

Elasmopus levis K. H. Barnard, 1916: 200, pl. 27, fig. 15.

Maera vagans K. H. Barnard, 1940: 459.

Records: Lüderitz (Penrith & Kensley 1970).

Diagnosis: Coxa 1 not acutely produced forwards; article 6 of gnathopod 2 longer than broad, palm oblique, irregularly dentate, most of the teeth bearing spines; third pleonal epimeron posteriorly smooth, postero-distally slightly produced; uropod 3 slightly exceeding 1 and 2, rami equal, lanceolate, apices acute, not setose.

Distribution: Endemic, Mossel Bay to Lüderitz.

Megaluropus namaquaeensis Schellenberg, 1953

Megaluropus namaquaeensis Schellenberg, 1953: 117, fig. 5.

Records: SWD 16J (4), SWD 18D (6), SWD 26C (200), SWD 27L (7), SWD 41K (8), SWD 51F (88); Walvis Bay (Schellenberg 1953).

Diagnosis: Gnathopods simple; gnathopod 2 with article 5 medially dilated, article 6 linear; uropod 3 exceeding uropod 1, rami equal, foliaceous, outer 1-articulate.

Distribution: Endemic, Saldanha Bay to Walvis Bay.

Melita appendiculata (Say, 1818)

Melita fresnelii: K. H. Barnard 1916: 189, pl. 28, fig. 32.

Melita appendiculata: J. L. Barnard 1970b: 161, figs 103, 104.

Records: SWD 21N (1), SWD 36G (2), SWD 37Q (1).

Distribution: Cosmopolitan.

Melita orgasmos K. H. Barnard, 1940

Melita orgasmos K. H. Barnard 1940: 454. Sivaprakasam, 1966: 114, fig. 12k-m.

Records: LU 54B (11), LU 112V (1); Lüderitz (Penrith & Kensley 1970).

Diagnosis: Upper apex of article 6 of gnathopod 1 overhanging base of dactyl; article 6 of gnathopod 2 ♂ longer than broad, palm transverse, shorter than hind margin, defined by a rounded lobe, otherwise smooth, dactyl normal; pleon segments 1-3 smooth, 4 produced into a slender median tooth, 5 with two submedian spines on each side.

Distribution: India, southern Africa.

Melita subchelata (Schellenberg, 1925)

Melita fresnelii var. *subchelata* Schellenberg, 1925: 153. K. H. Barnard, 1932: 211, fig. 130.

Records: SWD 61F (3), SWD 62F (6); Lüderitz (Schellenberg 1925); Walvis Bay (K. H. Barnard 1932).

Diagnosis: Upper apex of article 6 of gnathopod 1 not produced; article 6 of gnathopod 2 ♂ broader than long, palm transverse, as long as hind margin, a single tooth near finger hinge; dactyl massive, inner margin sinuous, distally hooked; pleon segments all dentate.

Distribution: Endemic to South West Africa.

Family **Haustoriidae***Bathyporeia* sp.

Bathyporeia gracilis: K. H. Barnard, 1951: 704 [non Sars 1891]

Records: SWD 18A (3), SWD 26L (4), SWD 27M (2), SWD 48Q (1), SWD 51E (11), SWD 56S (2).

Diagnosis: Antenna 2 of adult ♂ as long as body; apex of article 1 of antenna 1 broadly rounded with four or five feathery setae on the ventral margin; article 4 of pereopod 3 expanded.

Distribution: Endemic, False Bay to South West Africa.

Remarks: Barnard's material has been re-examined by Vader (1970) and found to differ from *B. gracilis* Sars, the main point of difference being that in *B. gracilis* Sars the antenna 2 ♂ is short, having only 12 flagellar articles. The material lies close to but is not identical with *B. tenuipes* and is to be described as a new species by Vader.

Urothoe grimaldi Chevreux, 1895

Urothoe grimaldii: Chevreux & Fage, 1925: 99, fig. 93. K. H. Barnard, 1955: 84, fig. 41b.

Records: SWD 41L (8).

Diagnosis: Accessory flagellum long, five-articulate; gnathopods similar, article

6 elongate, slender, with a short blunt palm; article 5 of pereopod 3 twice as wide as long; dactyl shaped like a pruning-knife, six to eight slender spines in a single row along the front margin.

Distribution: India, eastern Atlantic, Mediterranean.

Family **Isaeidae**

***Photis longidactylus* n. sp.**

Fig. 6

Description of male (5 mm): Head not quite as long as pereon segment 1; ocular lobes short, angular; eyes small, dark, composed of closely packed ommatidia; antenna 1 with ratio of peduncular articles 2:3:2, flagellum 7-articulate, accessory flagellum absent; antenna 2 equal to 1, article 2 produced ventrally, articles 4 and 5 equal, flagellum shorter than peduncle, 7-articulate.

Coxa 1 slightly produced forwards, 1.5 times as long as broad, coxae 2-4 similar in shape but slightly longer than coxa 1; article 2 of gnathopod 1 widening rapidly from a narrow attachment, article 6 hardly wider than, and about 1.2 times as long as article 2; palm slightly excavate, not defined, dactyl considerably longer than palm, cut into four teeth; gnathopod 2 with article 6 about 1.5 times as wide as article 2, palm concave, defined by a blunt process on the inner margin of the palm; dactyl extending beyond this process about halfway along hind margin of hand and closing outside the defining process, inner margin of dactyl cut into five teeth; pereopod 1 longer than 2, article 4 slightly shorter than article 2, anteriorly hirsute; articles 4 and 5 of pereopod 2 wider and stouter than those of pereopod 1; article 2 of pereopod 3 subrotund, article 6 distally with one large and one small spine, dactyl with a pair of accessory cusps; pereopod 4 similar to 3; pereopod 5 more elongate than 3 or 4, dactyl straight with two accessory cusps.

Pleonal epimera 1-3 smoothly rounded; uropods 1-3 terminating on the same plane; uropod 1 with its subequal lanceolate rami slightly upturned distally and $\frac{2}{3}$ length of peduncle; outer ramus of uropod 2 slightly shorter than inner, each with four dorsal spines and one long terminal spine, peduncle with a single distal spine on dorsal surface; outer ramus of uropod 3 subequal to peduncle, article 2 very short, with two small terminal spines and a group of setae lying alongside its origin, inner ramus less than 20% length of outer, terminating in one short spine; telson subquadrate, one seta at each distal corner.

Female: Ovigerous at 4 mm. Coxae much longer than those of the male, extending to end of article 2 of gnathopods and pereopods. Gnathopods smaller, but of similar structure to those of the male.

Holotype: SAM A13072, male, 5 mm.

Type-locality: SWD 51L, 26°37'S/15°07'E, 14 February 1963, depth 20 m, substrate fine muddy sand.

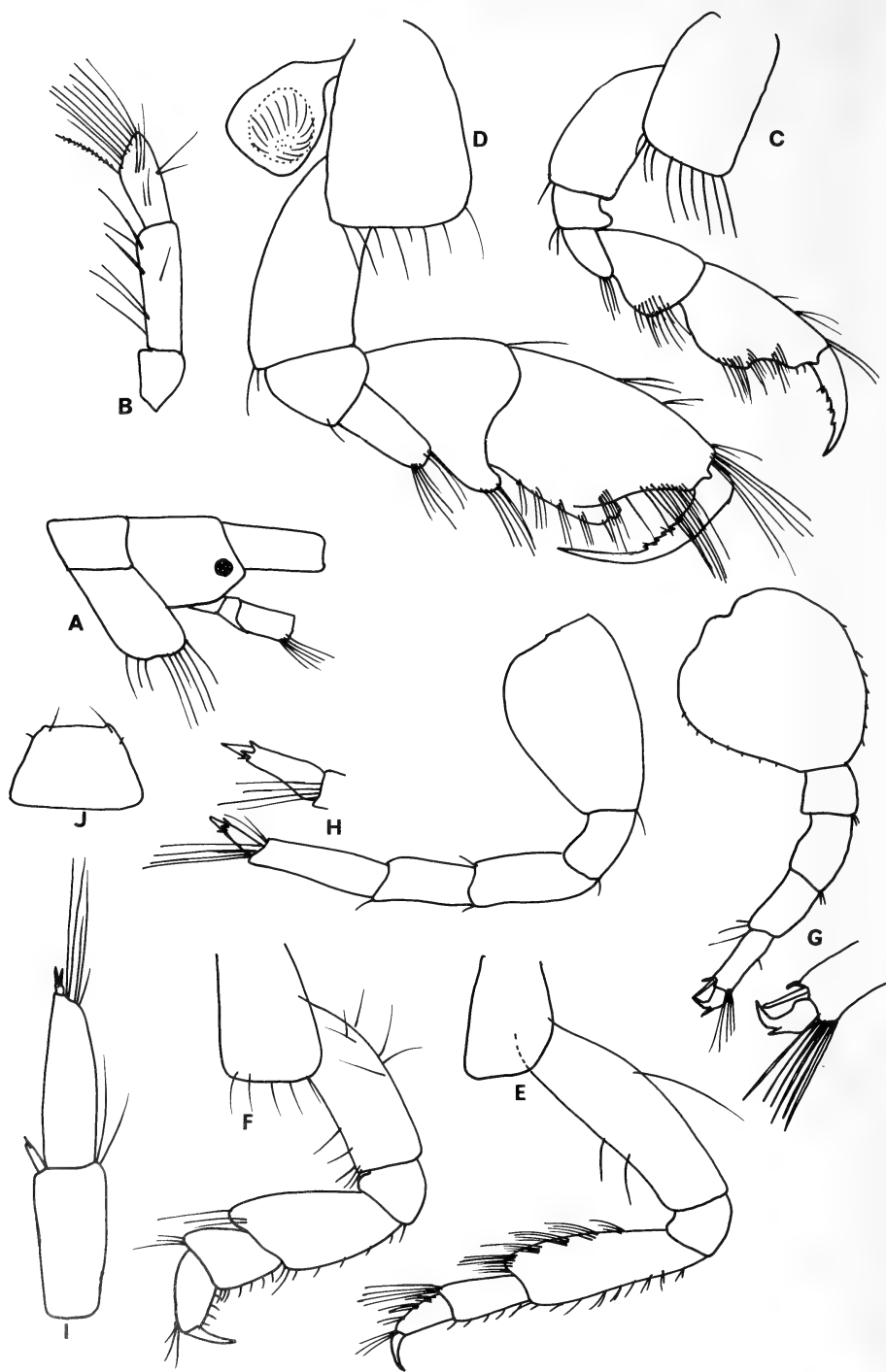


Fig. 6. *Photis longidactylus* n. sp., holotype, male, 5 mm:
 A. Head. B. Mandibular palp. C. Gnathopod 1. D. Gnathopod 2. E. Pereiopod 1. F. Pereiopod 2.
 G. Pereiopod 3 with tip of article 6 enlarged. H. Pereiopod 5 with tip enlarged. I. Uropod 3.
 J. Telson.

Remarks: Taxonomy of the genus *Photis* is complicated by the fact that males appear to pass through a series of developmental stages before attaining their terminal features. Despite the number of individuals which have been found, I have been unable to allocate these specimens to any known species. They bear some relationships to *P. africana* Schellenberg but have a longer dactyl to gnathopod 2 and lack a defining spine on gnathopod 1. Amongst southern African species they can be confused with *P. uncinata* Barnard, but lack the antero-distal process on article 2 of gnathopod 2 which characterizes that species.

Material: SWD 16P (1), SWD 18B (3), SWD 26D (39), SWD 40H (2), SWD 48S (1), SWD 51L (53), SWD 56T (3), SWD 58A (5).

Photis longimanus Walker, 1904

Photis longimanus: K. H. Barnard, 1916: 244. Sivaprakasam, 1970a: 567, fig. 8.

Records: SWD 30C (11), SWD 33C (12), SWD 36F (4), SWD 37M (21), SWD 51M (4), SWD 61D (21); Lüderitz (Schellenberg 1925).

Diagnosis: Gnathopod 2 ♂ with a large terminal rounded lobe on article 2 reaching to the tip of article 3; article 3 with a rounded lobe projecting horizontally inwards, palm very oblique, defined by a strong, elongate curved tooth, two other smaller teeth along the palmar margin.

Distribution: Southern Africa, India, Ceylon.

Remarks: The palmar teeth of these specimens are much more pronounced than those figured by Walker (1904) or Sivaprakasam (1970a). The defining tooth is strongly curved terminally and the other two teeth more elongate. The dactyl is shorter than the palm, whereas in Barnard's specimens it extended to the middle of the hind margin. These differences are probably growth changes—the present specimens of over 5 mm being larger than those of previous authors.

Family **Ischyroceridae**

Ischyrocerus anguipes Kröyer, 1838

Ischyrocerus anguipes: K. H. Barnard, 1916: 264. Schellenberg, 1953: 120, fig. 7a–c. J. L. Barnard, 1969: fig. 107b.

Records: SWD 21L; LU 52H (1); Lüderitz (Schellenberg 1953, Penrith & Kensley 1970).

Diagnosis: None of pereon segments dorsally carinate; article 2 of gnathopod 2 ♂ elongate, curved, anteriorly smooth, article 6 extremely large, elongate, palm almost parallel with convex anterior margin and bearing a broad denticulate tooth near finger hinge, dactyl smooth; rami of uropod 3 equal, the outer minutely hooked apically and bearing four or five small denticles on upper margin.

Distribution: Atlantic, Indo-Pacific.

Ischyrocerus carinatus K. H. Barnard, 1916

Ischyrocerus carinatus K. H. Barnard 1916: 266, pl. 28, fig. 18.

Records: Swakopmund (K. H. Barnard 1916).

Diagnosis: Pereon segments 1, 2, 6 and 7 each with a high mediodorsal carina; article 2 of gnathopod 2 ♂ remarkably elongate and slender, anterior margin proximally and distally serrate, article 6 of moderate size, narrow-oval, palm almost parallel with convex anterior margin and bearing a medial step and a distal bifid tooth, dactyl smooth; inner ramus of uropod 3 shorter than outer, outer ramus with an apical recurved spine and two minute dorsal denticles.

Distribution: Endemic, False Bay to South West Africa.

Ischyrocerus ctenophorus Schellenberg, 1953

Ischyrocerus ctenophorus Schellenberg, 1953: 121, fig. 7d-g.

Records: Lüderitz (Schellenberg 1953).

Diagnosis: None of pereon segments dorsally carinate; article 2 of gnathopod 2 ♀ (♂ unknown) elongate, anteriorly smooth, article 6 moderately elongate, palm oblique, defined by a narrow acute tooth, crenulate near finger hinge, dactyl with combs of setae on both faces; rami of uropod 3 equal, the outer almost as broad as long, bearing an apical spine and three large dorsal teeth.

Distribution: Endemic, the above record is unique.

Jassa falcata Montagu, 1808

Jassa falcata: Sexton & Reid, 1951: 30-47, pls 4-30. J. L. Barnard, 1969a: 155, figs 38-39.

Records: Swakopmund (K. H. Barnard 1916, Schellenberg 1925).

Diagnosis: Article 6 of gnathopod 2 ♂ elongate, hind margin ending in an enormous distally-directed acute process, palm bearing a stout tooth near finger hinge; rami of uropod 3 half length of peduncle, outer ramus bearing two dorsal flattened cusps and a large curved basally-immersed terminal spine; telson dorsally smooth.

Distribution: Cosmopolitan in shallow waters.

Jassa frequens (Chilton, 1883)

Jassa frequens: Schellenberg, 1953: 119, fig. 6.

Records: Lüderitz (Schellenberg 1953).

Diagnosis: Article 6 of gnathopod 2 ♂ oblong, hind margin ending in a square process distal to which the palm is deeply indented, palm otherwise smooth; rami of uropod 3 almost as long as peduncle, slender, nearly naked; telson with two or three sharp dorsal denticles.

Distribution: Chile, New Zealand, South West Africa.

Family **Leucothoidae***Leucothoe spinicarpa* (Abildgaard, 1789)

Leucothoe spinicarpa: K. H. Barnard, 1916: 148. Sivaprakasam 1967: 384, fig. 1.

Records: SWD 21E (6).

Distribution: Cosmopolitan.

Family **Liljeborgiidae***Listriella lindae* n sp.

Fig. 7

Description of male (8 mm): Lower anterior corner of head rounded and slightly produced, eyes oblique-oval, well developed, enclosed in a distinct capsule; antenna 1 extending to middle of article 4 of antenna 2, articles 1 and 2 of peduncle subequal, article 3 short, flagellum subequal to peduncle, 11-articulate; accessory flagellum 4-articulate, extending to article 3 of primary flagellum; antenna 2 as long as pereon, flagellum slightly shorter than peduncle, 15-articulate; article 1 of mandibular palp elongate but shorter than article 2 which is medially bent.

Palm of gnathopod 1 oblique, extremely convex, with a series of alternating small and large spines along its length, the longer spines with accessory cusps, hind margin separated from palm by an indistinct step; gnathopod 2 much larger than 1, palm defined by a single strong spine, finely setose throughout, a distinct step near finger-hinge (Fig. 7F); dactyl as long as palm, a distinct rugose hump on its inner margin opposite the palmar step; pereopods as in *L. goleta* J. L. Barnard.

Third pleonal epimeron upturned with a small notch at the postero-inferior corner; urosome segment 1 with a small dorsal tooth on its posterior margin, urosomite 2 with two such teeth; peduncle of uropod 1 with a large distal spine; rami of uropod 3 subequal, outer narrower than inner and with a small second article, four fascicles of spines along outer edge of basal article, inner margin of inner ramus proximally spinose, outer margin with a single row of small spines, seven strong spines around tip; telson with two large spines at apex of each lobe.

Colour (as preserved): Pereon and top of head uniform dark, otherwise white.

Holotype: SAM A13073, male, 8 mm.

Type-locality: SWD 40J, 26°36'S/15°06'E, 12 February 1963, depth 35 m, substrate fine sand.

Remarks: Gnathopod 2 of juveniles and females resembles gnathopod 1 in size and shape and has a more transverse, less convex palm than the adult male figured. Small specimens (3 mm) show a distinct dark brown band across article 3 of antenna 1 and article 4 of antenna 2 as well as various pereopod segments.

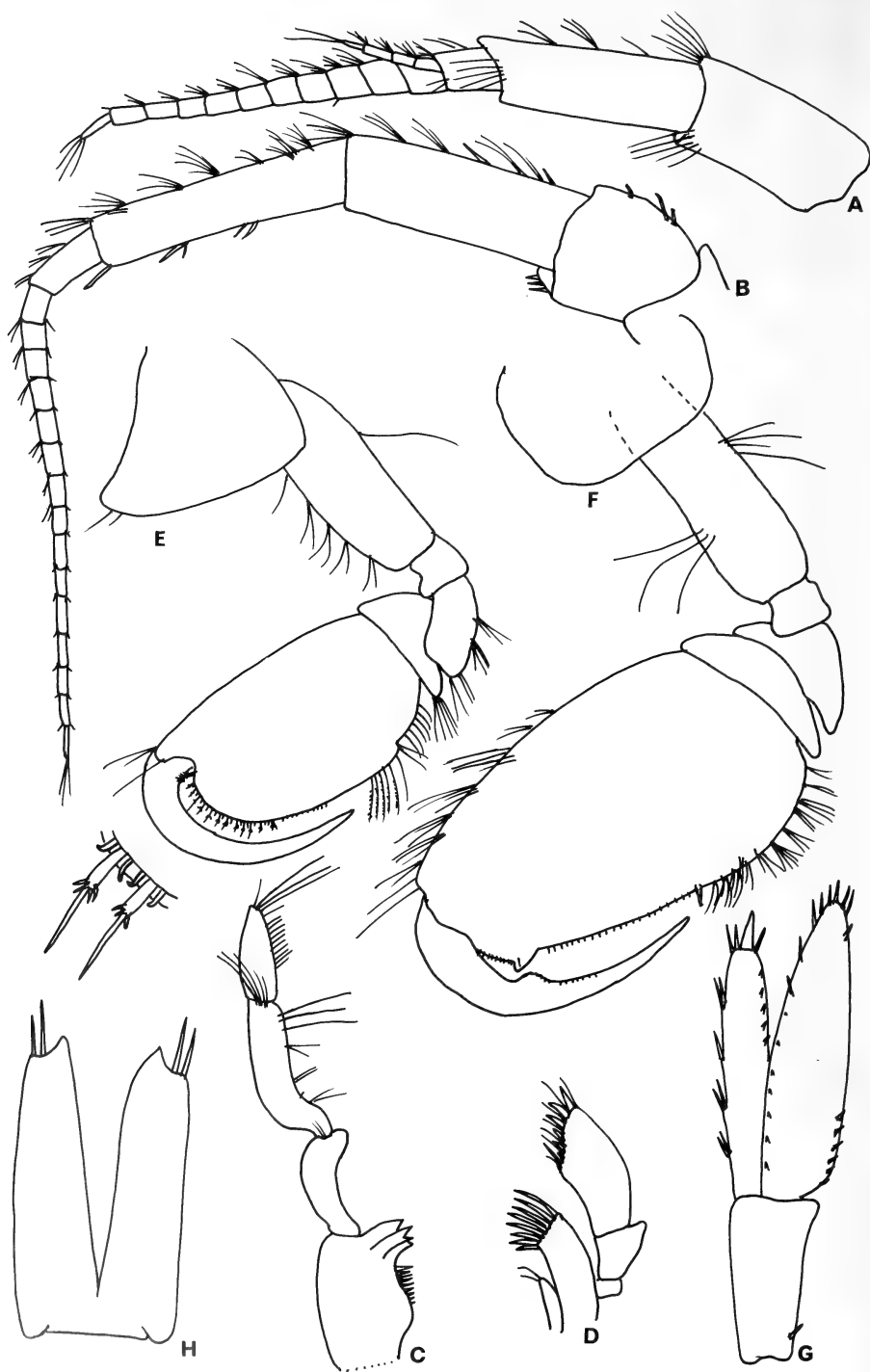


Fig. 7. *Listriella lindae* n. sp., holotype, male, 8 mm:
 A. Antennae 1. B. Antenna 2. C. Mandible. D. Maxilla 1. E. Gnathopod 1 with portion of palm enlarged. F. Gnathopod 2. G. Uropod 3. H. Telson.

This species can be distinguished from *L. albina* J. L. Barnard and *L. eriopisa* J. L. Barnard by virtue of its well-developed eyes. The very short article 2 of the outer ramus of uropod 3, the urosomal teeth and the oblique palm of gnathopod 2 male distinguish it from the other species of the genus. The closest known relative appears to be *L. goleta* J. L. Barnard but the spination of uropod 3 and form of gnathopod 2 are different.

Material: SWD 11N (3), SWD 16M (4), SWD 30A (9), SWD 33A (9), SWD 40J (2), SWD 41J (8), SWD 48T (1), SWD 49S (4), SWD 54J (3).

Family **Lysianassidae**

Amaryllis macrophthalma Haswell, 1880

Amaryllis macrophthalma: K. H. Barnard, 1916: 114.

Records: LU 56B (1), LU 99M (8), LU 101Y (2), LU 112V (1); SWA 2P (1).

Distribution: Indo-Pacific, extending to South West Africa.

Remarks: These specimens display a marked increase of the length of the flagellum of antenna 1 with size. A specimen of 4 mm had a 14-articulate flagellum, while one of 10 mm, had 26 articles to its flagellum.

Aristias symbiotica K. H. Barnard 1916

Aristias symbiotica K. H. Barnard, 1916: 122. Schellenberg, 1953: 111.

Records: Lüderitz (Schellenberg 1953).

Distribution: Endemic, Moçambique to South West Africa.

Cyphocaris challenger Stebbing, 1888

Cyphocaris challenger Stebbing, 1888: 661, pl. 17. Bowman & McCain 1967: 1-14, figs 1-9.

Records: 24°31'S 12°15'E (K. H. Barnard 1932).

Diagnosis: First pereon segment dorsally humped such that the top of the head faces forwards, the profile becoming lower and more rounded during development; hind margin of article 2 of pereopod 3 acutely produced to the tip of article 6, the process having 3-7 teeth on its upper surface, none on its lower; article 2 of pereopods 4 and 5 posteriorly cut into 14 and 13 strong teeth respectively; uropod 3 extending beyond the telson.

Distribution: Cosmopolitan, pelagic 25-200+ m.

Lysianassa ceratina (Walker, 1889)

Lysianassa cubensis: K. H. Barnard, 1916: 120.

Lysianassa ceratina: Chevreux & Fage, 1925: 42, fig. 23. Reid, 1951: 194.

Records: SWD 10B (1); LU 8C (1), LU 41B (1), LU 61Z (4), LU 86Z (1), LU 94C (4), LU 101Y (2), LU 103M (4), LU 112Q (2), LU 114Y (3), LU 121L (31); Lüderitz (Schellenberg 1925, Penrith & Kensley 1970).

Diagnosis: Article 1 of antenna 1 twice as long as wide, a flat lateral tooth on inner margin, accessory flagellum 5-articulate; eyes large, vertically elongate; third pleonal epimeron postero-distally rounded; inner ramus of uropod 2 strongly constricted; peduncle of uropod 3 strongly keeled, rami shorter than peduncle, subequal; telson oval, entire.

Distribution: Eastern Atlantic, Mediterranean, southern Indian Ocean.

Lysianassa minimus (Schellenberg, 1953)

Proannonyx minimus Schellenberg, 1953: 108, fig. 1.

Records: Lüderitz, Walvis Bay (Schellenberg 1953).

Diagnosis: Article 1 of antenna 1 twice as long as wide, without lateral tooth, accessory flagellum 2-articulate; eyes small, round; third pleonal epimeron postero-distally rounded-quadrate; inner ramus of uropod 2 simple; peduncle of uropod 3 with a plate-like distal expansion, outer ramus equal to peduncle, inner ramus shorter than outer; telson rounded, entire.

Distribution: Endemic, known only from the above records.

Lysianassa variegata (Stimpson, 1855)

Lysianassa variegata: Stebbing, 1888: 682, pl. 23.

Records: LU 61Z (1); Lüderitz (Penrith & Kensley 1970).

Diagnosis: Article 1 of antenna 1 twice as long as wide, without lateral tooth, accessory flagellum 4-articulate; eyes large, dark, vertically elongate; third pleonal epimeron postero-distally upturned with a small tooth; inner ramus of uropod 2 simple; peduncle of uropod 3 faintly keeled, rami shorter than peduncle, the outer slightly the longer; telson subquadrate, notched.

Distribution: Africa south of the equator.

Orchomene plicata (Schellenberg, 1925)

Orchomenopsis chilensis: Schellenberg, 1925: 119, fig. 3. K. H. Barnard, 1925: 330.

Orchomenella plicata: K. H. Barnard, 1940: 440.

Records: SWD 26K (24); Lüderitz (Schellenberg 1925).

Diagnosis: Eyes elongate oval, nearly meeting on top of head, third pleonal epimeron quadrate; telson twice as long as broad, $\frac{4}{5}$ cleft; article 1 of antenna 1 very stout, almost as broad as long and twice as long as articles 2 plus 3, flagellum 10-12 articulate, accessory flagellum 6-articulate; gnathopod 1 stout, article 2 twice as long as broad, article 5 very short with a narrow apical posterior lobe, palm transverse, cut into four or five little teeth; lower apex of article 5 of gnathopod 2 produced into an acute thumb, dactyl straight, closely fitting; article 4 of pereopods 3 and 4 strongly expanded posteriorly.

Distribution: Cosmopolitan.

Tryphosella normalis (K. H. Barnard, 1955)

Tryphosa normalis K. H. Barnard, 1955; 80, fig. 39.

Records: SWD 49V (1).

Diagnosis: Eyes absent; third pleonal epimeron postero-inferiorly bluntly quadrate; first urosomite with a rounded dorsal hump; palm of gnathopod 1 very oblique, almost as long as hind margin, defined by two slender spines; telson with two pairs of dorsal spines and a pair of small spines at apex of each lobe.

Distribution: Endemic, False Bay to Lüderitz.

Family **Ochlesidae***Ochlesis levetzowi* Schellenberg, 1953

Ochlesis levetzowi Schellenberg, 1953: 115, fig. 4. J. L. Barnard, 1969b: 372, fig. 134a.

Records: Lüderitz, Walvis Bay (Schellenberg 1953).

Diagnosis: Maxillipedal palp absent; pleon segments not posteriorly carinate; third pleonal epimeron postero-inferiorly quadrate, not upturned; peduncular articles of antenna 1 not ventrally produced.

Distribution: Endemic to South West Africa.

Family **Oedicerotidae***Periocolodes longimanus* (Bate & Westwood, 1868)

Periocolodes longimanus: Chevreux & Fage, 1925: 162, figs 162-3. Ledoyer, 1967: 127, fig. 7.

Records: SWD 16L (100), SWD 18E (3), SWD 26A (195), SWD 27J (12), SWD 30D (2), SWD 33D (2), SWD 36D (5), SWD 37R (6), SWD 40K (8), SWD 41G (15), SWD 46H (1), SWD 49U (1), SWD 51G (125), SWD 56R (1), SWD 62D (22), SWD 72L (1).

Distribution: Mediterranean, Atlantic and Indian Oceans.

Family **Phliantidae***Temnophlias capensis* K. H. Barnard, 1916

Temnophlias capensis K. H. Barnard, 1916: 158, pl. 26, figs 25-35.

Records: LU 53M (3).

Diagnosis: Pereon smooth, coxae subrectangular; pleon segment 2 ♂ with a pair of anterior submedian tubercles, a second pair near the posterior margin, posterior margin of segment ventrally produced backwards as a rounded lobe overhanging segment 3; pereopods 1-3 of ♂ chelate, 4 and 5 simple.

Distribution: Endemic, Still Bay to South West Africa.

Family **Podoceridae***Laetmatophilus purus* Stebbing, 1888

Laetmatophilus purus Stebbing, 1888: 1198, pl. 132. K. H. Barnard, 1916: 274.

Records: SWD 21S (500), SWD 39P (16).

Podocerus africanus K. H. Barnard, 1916

Podocerus africanus K. H. Barnard, 1916: 278, pl. 28, figs 24-25; 1925: 367; 1937: 176, fig. 19.

Records: LU 52G (1).

Diagnosis: Body not carinate, article 4 of gnathopod 2 ♂ strongly and acutely produced, palm with a short area of plumose setae distally and two strong teeth near the hinge; antero-distal margin of article 2 of pereopods 1 and 2 lobed; article 2 of pereopods 3-5 widest at base and tapering distally.

Distribution: South Arabian coast, Natal to South West Africa.

Podocerus cristatus (Thompson, 1879)

Podocerus cristatus: K. H. Barnard, 1916: 276. J. L. Barnard, 1962: 67, fig. 31.

Records: Swakopmund (Schellenberg 1925).

Distribution: Cosmopolitan in tropical and warm temperate seas.

Family **Stenothoidae***Stenothoe valida* Dana, 1853

Stenothoe affinis: K. H. Barnard, 1925: 345.

Stenothoe valida: Ledoyer, 1967: 125, fig. 4b. Sivaprakasam, 1967: 373, fig. 2a-b.

Records: LU 112V (1).

Distribution: Cosmopolitan in tropical and temperate seas.

Superfamily TALITROIDEA

Family **Hyalidae***Allorchestes inquirendus* K. H. Barnard, 1940

Allorchestes inquirendus K. H. Barnard, 1940: 477, fig. 34b-c.

Records: LU 8B (1), LU 55A (1), LU 105C (2), LU 106D (4), LU 107A (1), LU 108B (1), LU 112P (10) 114X (7); SWA 4J (2).

Diagnosis: Article 5 of gnathopod 2 ♂ lobed, the lobe extending between articles 4 and 5; palm oblique, defined by a pocket-like cavity and two spines, hind margin quite long.

Distribution: Endemic, Port Elizabeth to South West Africa.

Hyale diastoma K. H. Barnard, 1916

Hyale diastoma K. H. Barnard, 1916: 232, pl. 28, fig. 8.

Records: LU 52F (1), LU 56C (3), LU 57H (1), LU 61W (4), LU 99L (1), LU 103L (4), LU 112V (13); Lüderitz (Penrith & Kensley 1970).

Diagnosis: Antenna 1 extending to centre of flagellum of antenna 2, articles 1 and 2 not distally lobed; coxae 1-4 with triangular process at centre of hind margins; article 2 of gnathopod 2 ♂ with large anterior lobe, article 3 not lobed, palm nearly transverse, sinuous, defined by two spines, dactyl stout, inner margin sinuous; article 2 of pereopod 5 subcircular, bearing a few posterior setiferous indents.

Distribution: Endemic, False Bay to South West Africa.

Hyale grandicornis Kröyer, 1845

Hyale grandicornis: K. H. Barnard, 1916: 230. Stephensen, 1949: 33, figs 14-15. K. H. Barnard, 1955: 93, fig. 46.

Records: LU 33T; Lüderitz (Penrith & Kensley 1970).

Distribution: Indo-Pacific, southern Atlantic.

Hyale hirtipalma (Dana, 1852)

Hyale hirtipalma: K. H. Barnard, 1916: 234. Stephensen, 1949: 30, fig. 13.

Records: LU 52H (4), LU 54E (1), LU 57H (1), LU 86Y (5), LU 101W (1), LU 106C (1), LU 112N (7); SWA 2N (1); Lüderitz (Penrith & Kensley 1970).

Diagnosis: Antenna 1 extending $\frac{1}{3}$ way along flagellum of antenna 2, articles 1 and 2 not distally lobed; coxae 1-4 with triangular process at centre of hind margin; article 2 of gnathopod 2 ♂ with a large anterior lobe, article 3 not lobed, palm very oblique, strongly setose, defined by two spines, dactyl evenly tapering; article 2 of pereopod 5 oval, posteriorly faintly crenulate.

Distribution: Pacific, South Atlantic.

Hyale macrodactyla Stebbing, 1899

Hyale macrodactyla: K. H. Barnard, 1916: 235. Sivaprakasam, 1969: 308.

Records: LU 52H (12), LU 54C (26), LU 61Y (15), LU 101V (5), LU 103J (14), LU 112M (22).

Diagnosis: Antenna 1 extending $\frac{1}{3}$ way along flagellum of antenna 2, articles 1 and 2 not distally lobed; coxae 1-4 posteriorly smooth; articles 2 and 3 of gnathopod 2 ♂ anteriorly lobed, palm very oblique, bordered on both sides by rows of slender spinules, defined by two spines in a pocket, dactyl widest medially, reaching end of article 4; article 2 of pereopod 5 circular, posteriorly serrate.

Distribution: India, southern Atlantic.

Hyale saldanha Chilton, 1912

Hyale saldanha Chilton, 1912: 509, pl. 2, figs 24-29. K. H. Barnard, 1916: 229, pl. 27, fig. 37.

Records: LU 33S (1), LU 52E (6), LU 54D (6), LU 61X (12), LU 82Q (1), LU 99K (5), LU 101X (4), LU 103H (13), LU 105B (1), LU 112 L (10); SWA 1P (6); Lüderitz (Schellenberg 1925, Penrith & Kensley 1970).

Diagnosis: Antenna 1 extending $\frac{1}{3}$ way along flagellum of antenna 2, articles 1 and 2 distally lobed; coxae 1-4 posteriorly smooth; articles 2 and 3 of gnathopod 2 ♂ anteriorly lobed, palm oblique, straight except for a small lobe near the hinge, defined by two spines in a pocket; dactyl evenly tapering, equal to palm; article 2 of pereopod 5 circular, smooth.

Distribution: Endemic, East London to South West Africa.

Orchestia rectipalma (K. H. Barnard, 1940)

Parorchestia rectipalma K. H. Barnard, 1940: 473, fig. 32.

Records: LU 34F (15), LU 36B (7).

Diagnosis: Scabrous lobes on articles 4 to 6 of gnathopod 1 ♂, article 6 of gnathopod 2 ♂ widest at defining angle, palm straight, separated from the hind margin by a distinct step carrying a short strong spine, dactyl evenly convex, fractionally longer than palm; article 2 of pereopod 5 with very faint setiferous serrations posteriorly.

Distribution: Endemic, Natal to South West Africa.

Talorchestia australis K. H. Barnard, 1916

Talorchestia australis K. H. Barnard, 1916: 220, pl. 27, figs 33-34; 1940: 470, fig. 30.

Records: Lüderitz (Penrith & Kensley 1970).

Distribution: Moçambique to South West Africa.

Talorchestia quadrispinosa K. H. Barnard, 1916

Talorchestia quadrispinosa K. H. Barnard, 1916: 217, pl. 27, figs 29-32.

Records: LU 8A (1), LU 64C (5), LU 66A (1); OR 2 (fairly common); Walvis Bay, Prince of Wales Bay (Schellenberg 1925); Lüderitz (Penrith & Kensley 1970).

Diagnosis: Eyes separated dorsally by less than their diameter; coxa 2 not lobed; pleon segments 1 and 2 (and sometimes 3) each with 2 medio-dorsal tubercles in adult ♂; article 4 of gnathopod 1 ♂ not lobed, article 5 distally lobed, article 6 shorter than 5, not widening much distally; palm of gnathopod 2 ♂ distally concave, a strong triangular tooth near the hinge, defined by a tubercle from short hind margin; dactyl as long as palm or extending well beyond it, slightly emarginate proximally.

Distribution: Endemic, False Bay to South West Africa.

Suborder CAPRELLIDEA

Family **Caprellidae***Caprella danilevskii* Czerniavski, 1868

Caprella danilevskii: Chevreux & Fage, 1925: 454, fig. 432. McCain, 1968: 22-25, figs 10-11.

Records: Swakopmund (K. H. Barnard 1916).

Diagnosis: Head elongate, anteriorly rounded-quadrate; article 2 of gnathopod 2 shorter than pereon segment 2, article 6 elongate, palm oblique, equal to hind margin, bearing a distal rectangular tooth and defined by a poison tooth, dactyl shorter than palm; gills elliptical, long axis usually parallel to body, pereopods 3-5 lacking grasping spines.

Distribution: Widespread, pan-tropical.

Caprella equilibra Say, 1818

Caprella equilibra: McCain, 1968: 25-30, figs 12-13.

Records: SWD 21R (37), SWD 26F (1), SWD 27H (3), SWD 39R (38); Swakopmund (K. H. Barnard 1916).

Distribution: Cosmopolitan 0-300 m.

Caprella penantis Leach, 1814

Caprella penantis: McCain, 1968: 33-40, figs 15-16.

Records: Lüderitz (Penrith & Kensley 1970).

Diagnosis: Head short, bearing a large triangular antero-dorsal process; article 2 of gnathopod 2 shorter than pereon segment 2, palm occupying almost whole length of hand, bearing a rectangular projection near hinge and defined by a poison tooth, dactyl equal to palm; gills subcircular, pereopods 3-5 each with a pair of grasping spines.

Distribution: Cosmopolitan in tropical and temperate seas.

Caprella scaura Templeton, 1836

Caprella scaura: K. H. Barnard, 1925: 371. McCain, 1968: 40-44, figs 17-18.

Records: LU 113N (1).

Distribution: Cosmopolitan.

Family **Phtisicidae***Phtisica marina* Slabber, 1769

Phtisica marina: K. H. Barnard, 1916: 283. McCain, 1968: 91-97, figs 46-47.

Records: SWD 21Q (12), SWD 26E (3), SWD 39Q (1), LU 121M (1).

Distribution: Atlantic, Black Sea, Mediterranean, east coast of southern Africa.

Caprellina longicollis (Nicolet, 1849)

Caprellina longicollis: McCain, 1969: 289, fig. 2.

Records: Lüderitz (Penrith & Kensley 1970).

Diagnosis: Body dorsally smooth, a pair of antero-lateral projections on pereon segments 2 and 3; palm of gnathopod 2 ♂ half as long as hand, cup-shaped distally; pereopods 1 and 2 absent, pereopod 3 three or four-segmented.

Distribution: Southern oceans, Mediterranean.

Caprellina spiniger K. H. Barnard, 1916

Caprellina spiniger K. H. Barnard, 1916: 282, pl. 28, fig. 35; 1955: 99.

Records: Lüderitz (Penrith & Kensley 1970).

Diagnosis: Pereon segment 3 bearing a forward-directed longitudinally-bifid dorsal tubercle, segments 2 and 4 sometimes with similar but smaller tubercles; a pair of antero-lateral spines on pereon segment 2 above insertion of gnathopod 2; gnathopod 2 as in *C. longicollis*; pereopods 1 and 2 absent, pereopod 3 of 3 segments.

Distribution: Endemic, False Bay to Lüderitz.

SUMMARY

The records of the University of Cape Town Ecological Survey have been incorporated with the findings of previous workers in listing the known gamma-reidean and caprellid amphipod fauna of South West Africa south of 20°S.

Eighty-one species are recognized in all. Of these five are presented here as new to science, namely *Guernea rhomba* n. sp., *Eriopisa epistomata* n. sp., *Eriopisella epimera* n. sp., *Photis longidactylus* n. sp. and *Listriella lindae* n. sp. A further 26 species are recorded from South West Africa for the first time. References and synonyms are given for all the species and short diagnoses for those not described in Part I of this series.

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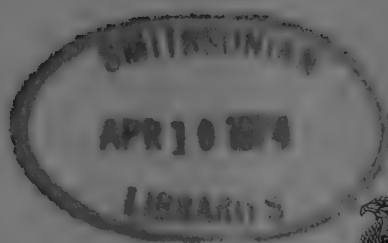
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PART 3

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By

C. L. GRIFFITHS

C.S.I.R. Oceanographic Research Unit, University of Cape Town

(With 8 figures)

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INTRODUCTION

The aim of this third paper in the series on the benthic Amphipoda of southern Africa is to bring together existing information concerning the marine gammaridean and caprellid amphipod fauna of Natal. The main body of data has been drawn from the collections of the University of Cape Town Ecological Survey and of the National Institute for Water Research of the South African Council for Scientific and Industrial Research. To these have been added the records of previous workers in the area, notably T. R. R. Stebbing (1918), K. H. Barnard (1916, 1925, 1940) and J. L. Barnard (1961).

A considerable number of estuaries are situated along the Natal coast and these have been the subject of much of the collecting effort in the area. As a result the estuarine fauna is well known while the marine environment has been less thoroughly sampled. Collecting in deeper waters has been particularly neglected, indeed the area between 200 and 1 000 m remains virtually untouched and there can be little doubt that many new species await discovery there.

The Natal seaboard is of a subtropical type, being warmed by the southerly flowing Agulhas current. The continental shelf is narrow, except in the stretch between Richard's Bay and Durban, and hence the current flows close inshore and has a profound effect upon the littoral fauna. The mean sea temperature is in fact maintained at a level some 10°C higher than found at the same latitude on the west coast, the normal range being between about 25°C in summer and 19°C in winter.

The collecting areas of the University of Cape Town and National Institute for Water Research (NIWR) are described briefly below and shown on Figure 1.

THE COLLECTING STATIONS

The various collections incorporated into this survey are best considered as falling into two groups—those from estuaries and brack-water lakes, and those from the open sea. Each of these categories is further divided according to the source of the samples.

Samples from the open sea

(a) Collections of the National Institute for Water Research (NIWR)

This series of some 50 benthic samples was collected by the R.V. *Meiring Naudé* on behalf of the National Institute for Water Research of the South African Council for Scientific and Industrial Research. Amphipods were recovered from 36 of these samples and kindly loaned to the author for identification. Examination of the samples revealed 47 recognizable species including four new to science and two others (*Ampelisca miops* and *Metaprotella macrodactylos*) previously known only from the holotype. Most of the samples were dominated by burrowing species, the most common being *Mandibulophoxus stimpsoni*, which was present in 22 of the samples. Other prominent species were *Byblis gaimardi*, *Microdeutopus thubellinus* n. sp., *Ampelisca diadema* and *Unciolella spinosa* n. sp.

Station data for samples containing amphipods are provided below. The samples were collected on three separate cruises and this is reflected in the catalogue numbers which are coded: NIWR/cruise/station number, the cruises being referred to as 1 and 2 and 'Umlass' (UM). Thus, station NIWR/1/3 is the third sample from cruise 1.

N.I.W.R. station data

<i>Catalogue no.</i>	<i>Date</i>	<i>Location</i>	<i>Depth (m)</i>
NIWR/1/3	15/5/72	28°36'S/32°26'E	55
NIWR/1/5	15/5/72	28°48'S/32°11'E	32
NIWR/1/6	15/5/72	28°48'S/32°11'E	50
NIWR/1/9	15/5/72	28°56'S/32°01'E	22

<i>Catalogue no.</i>	<i>Date</i>	<i>Location</i>	<i>Depth</i> (m)
NIWR/1/13	15/5/72	29°34'S/31°17'E	48
NIWR/1/14	15/5/72	29°34'S/31°17'E	53
NIWR/1/15	15/5/72	29°34'S/31°17'E	60
NIWR/1/24	15/5/72	30°21'S/30°52'E	52
NIWR/1/26	15/5/72	30°36'S/30°37'E	52
NIWR/1/27	15/5/72	30°37'S/30°40'E	58
NIWR/2/17	19/7/72	30°03'S/30°58'E	52
NIWR/2/18	19/7/72	30°04'S/30°01'E	155
NIWR/2/19	19/7/72	30°13'S/30°49'E	19
NIWR/2/20	19/7/72	30°14'S/30°52'E	44
NIWR/2/21	19/7/72	30°15'S/30°55'E	148
NIWR/2/22	19/7/72	30°19'S/30°45'E	23
NIWR/2/23	19/7/72	30°20'S/30°48'E	60
NIWR/2/24	19/7/72	30°21'S/30°52'E	102
NIWR/2/25	19/7/72	30°35'S/30°35'E	38
NIWR/2/27	19/7/72	30°37'S/30°40'E	71
NIWR/2/28	19/7/72	30°45'S/30°29'E	32
NIWR/2/29	19/7/72	30°46'S/30°31'E	49
NIWR/2/30	19/7/72	30°47'S/30°33'E	56
NIWR/2/31	19/7/72	30°53'S/30°23'E	32
NIWR/2/32	19/7/72	30°53'S/30°26'E	50
NIWR/2/33	19/7/72	30°54'S/30°29'E	86
NIWR/2/35	19/7/72	31°04'S/30°17'E	42
NIWR/2/36	19/7/72	31°05'S/30°19'E	72
NIWR/UM/P5	15/9/70	29°59'S/31°03'E	60
NIWR/UM/O3	15/9/70	29°59'S/31°03'E	51
NIWR/UM/R3	15/9/70	29°59'S/31°03'E	55
NIWR/UM/P1	15/9/70	29°59'S/31°03'E	25
NIWR/UM/M4	15/9/70	29°59'S/31°03'E	55
NIWR/UM/M1	3/11/72	29°59'S/31°03'E	30
NIWR/UM/M2	3/11/72	29°59'S/31°03'E	40
NIWR/UM/M3	3/11/72	29°59'S/31°03'E	50

(b) *Natal dredge (NAD)*

Benthic samples from Natal in the collections of the University of Cape Town are denoted by this code. To date there are 93 samples in the series, ranging from 18 to 200 m in depth. Only 24 of the samples include amphipods, a total of 39 species being recorded. Although this is a considerable number of species it is notable that 32 of them were recorded only in one sample and that the total number of individuals is small. This, coupled with the fact that species most common in the NIWR series (above) are generally poorly represented or absent in the NAD samples, indicates that a large number of benthic species are still to be found in the area.

Tube-building forms such as *Ampelisca brevicornis*, *A. spinimana*, *A. anisuropa* and *Photis kapapa* dominated sandy and muddy samples in the series, while *Eusiroides monoculodes* was common in rocky areas. The two best represented species in the series, *Gammaropsis atlantica* and *Melita appendiculata* occurred in both hard and soft substrate areas.

Station data for those samples in which amphipods were represented are given below.

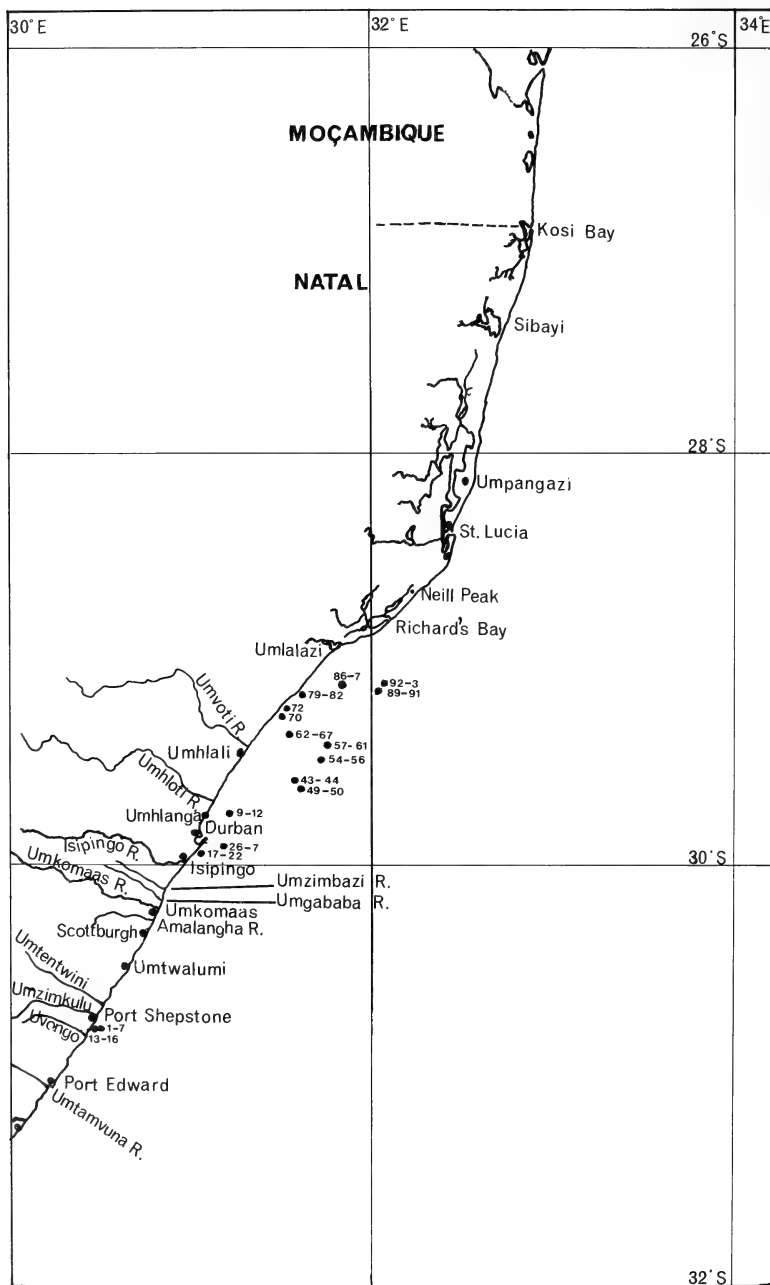


Fig. 1. Collecting stations along the Natal coast. Numbers represent NAD stations.

NAD station data

Catalogue no.	Date	Location	Depth (m)	Substrate	Gear
NAD 4	17/5/58	30°47'S/30°29'E	44	Stones	—
NAD 7	17/5/58	30°47'S/30°29'E	44	Stones	—
NAD 11	23/4/58	29°46'S/31°17'E	110	Stones	—
NAD 12	23/4/58	29°46'S/31°17'E	110	—	—
NAD 15	13/8/58	30°47'S/30°27'E	36	—	—
NAD 16	13/8/58	30°47'S/30°27'E	36	—	—
NAD 19	12/8/58	29°58'S/31°02'E	49	—	—
NAD 27	13/7/59	29°53'S/31°06'E	71	Mud	Dredge
NAD 39	9/9/64	29°35'S/31°38'E	150	Sandy mud	Grab
NAD 43	9/9/64	29°34'S/31°39'E	115	Sandy mud	Grab
NAD 49	9/9/64	29°35'S/31°42'E	138	Coral, gravel	Grab
NAD 56	9/9/64	29°29'S/31°45'E	86	Mud	Grab
NAD 57	9/9/64	29°26'S/31°46'E	77	Mud	Dredge
NAD 61	9/9/64	29°26'S/31°46'E	77	Mud	Grab
NAD 64	9/9/64	29°21'S/31°36'E	57	Shelly sand	Dredge
NAD 66	9/9/64	29°21'S/31°36'E	57	Shelly sand	Grab
NAD 70	9/9/64	29°18'S/31°33'E	47	Mud	Grab
NAD 72	10/9/64	29°16'S/31°32'E	35	Mud	Grab
NAD 81	29/7/64	29°11'S/31°37'E	18	Rock	Dredge
NAD 86	29/7/64	29°10'S/31°51'E	43	Sand	Trawl
NAD 90	30/7/64	29°11'S/32°02'E	70	Rock shell	Dredge
NAD 92	30/7/64	29°10'S/32°05'E	170	Rock, sand	Grab

(c) Shore stations

Early shore collections made by the University of Cape Town are denoted by single letter codes. Five stations in this series fall into our area: Umpangazi (G), Umhlati (U), Durban (D), Umtwalumi (M) and Port Edward (W). The records are purely of a presence—absence type, no data on abundance having been kept. Of the 13 species recorded, *Hyale grandicornis* and *Elasmopus pecteniscrus* appear to be the best distributed.

More recently shore samples have been lumped together under a single code (NA). Only five NA samples include amphipods, 17 species being found in all. The fact that the last of these samples added eight species to the list gives some indication of the inadequacy of the sampling coverage to date. The position at present indicates that the most common rocky intertidal species are *Maera inaequipes*, *Caprella penantis*, *Podocerus africanus*, *Jassa falcata* and *Hyale grandicornis*.

NA station data

Catalogue no.	Date	Location
NA 189	13/7/56	Port St. Johns, general collection
NA 191	13/7/56	Port St. Johns, general collection
NA 205	13/7/56	Port St. Johns, general collection
NA 243	25/7/72	Umhlanga, general collection from weeds
NA 244	27/7/72	Scottburgh, general collection from weeds

(d) Anton Bruun dredge (ABD)

A small collection of dredge samples collected by the S.S. *Anton Bruun* during 1964 is allocated to this code. Very few of the stations fall into the area

under consideration here, and from these only one amphipod, *Monoliropus falcimanus* Mayer, is recorded.

ABD station data

<i>Catalogue no.</i>	<i>Date</i>	<i>Location</i>	<i>Depth</i>
ABD 14	8/9/64	29°45'S/31°40'E	440 m

Samples from estuarine areas

(a) *Kosi Bay (KOS)*

A preliminary survey of Kosi Bay has been conducted by Broekhuysen & Taylor (1959), while details of the benthos of Nhlangwe and Sifungwe Lakes have been investigated by Bolt (1969b). The system is composed of a series of lakes running from south-west to north-east and opening to the sea just south of the Mozambique border. Two rivers flow into the uppermost and largest lake, Lake Nhlangwe, and this is joined to the smaller Sifungwe and Mponawini Lakes by a narrow winding channel. These in turn communicate with a tidal basin into which two further rivers discharge and which is connected to the sea by a short straight channel about 20 m wide.

At the time of Broekhuysen & Taylor's (1959) original survey the water in the system was exceptionally clear. Salinity in the tidal basin varied between 10 and 16‰ compared with 6–8‰ in Mponawini and Sifungwe and 3‰ in Nhlangwe, while water temperatures fell between 20 and 24°C. Full details of physical and biological features of the lakes at the time of sampling may be found in Broekhuysen & Taylor (1959).

In 1966 the Kosi system was flooded during a cyclone which raised the water level some 2 m before the sandbar at the mouth opened. This inundation caused a considerable accumulation and subsequent decay of organic matter in Lake Nhlangwe and several years passed before the water cleared fully. Details of the recovery of the lakes after these floods may be found in Bolt (1969b).

Four species of amphipod were recorded in the system by Broekhuysen & Taylor (1959) and to these Bolt (1966) has added two further benthic species. Of the six species *Urothoe serrulidactylus* is found only in the sandy shallows of Lake Sifungwe. *Afrochiltonia capensis* and *Melita zeylanica* are distributed throughout the upper reaches of the system, while *Orchestia ancheidos* is common along the driftline. The benthos of the lakes is dominated by *Grandidierella bonnierii* and *Corophium triaenonyx*. These two species have increased greatly in both density and range as conditions have improved following the floods of 1966, reaching a density of over 1 000 m/sq. in places by 1969.

Kosi Bay station data

<i>Catalogue no.</i>	<i>Date</i>	<i>Location</i>
KOS 6	18/4/48	Nhlangwe Lake, shore
KOS 15	12/7/49	Shore of tidal basin
KOS 53	15/7/49	Northern tip of Nhlangwe Lake

<i>Catalogue no.</i>	<i>Date</i>	<i>Location</i>
KOS 52	16/7/49	Between tidal basin and Mpunowini Lake
KOS 69	17/7/49	Between tidal basin and Mpunowini Lake
KOS 74	17/7/49	Shore of Mpunowini Lake
KOS 78	18/7/49	Shore of Mpunowini Lake
KOS 81	18/7/49	Shore of Sifungo Lake
KOS 82	18/7/49	Shore of Sifungo Lake
KOS 83	19/7/49	Shore of Sifungo Lake

(b) *St. Lucia* (STL)

The main body of the St. Lucia system is a saline lake shaped like the letter H and about 18 km wide by 40 km long, the western limb being known as False Bay, the crosspiece as Hell's Gates and the eastern limb as Lake St. Lucia proper. The eastern limb of the lake is further subdivided into the North Lake from which elongate shallow South Lake is almost completely separated by an island known as Fanie's Island. On the western shore of the South Lake lies the settlement of Charter's Creek and from its southern tip winds a long narrow channel some 15 km long and seldom more than 2 m deep. Some 2 km from the mouth of this channel lies the village of St. Lucia, reached by a bridge across the channel. At the time of sampling the large Umfolosi River flowed into the system just before its junction with the sea but the river mouth has since been diverted south.

Several rivers flow into the main lake, notably the Hluhluwe, flowing into False Bay and the Mkuze, which enters North Lake. Variations in rainfall and evaporation cause wild fluctuations of depth, salinity and substrate in the system. However, the bottom is chiefly muddy and the depth of the lake averages 1 m or less. Salinity is generally higher than that of the sea but falls violently when the system is flushed by heavy rains. Considerable water turbidity is normal while temperatures generally fall between 20° and 30°C.

Two surveys of the lake system have been undertaken by the University of Cape Town resulting in the publications of Day, Millard & Broekhuysen (1953) and Millard & Broekhuysen (1965). Detailed descriptions of the physical and biological conditions at the times of sampling (1948-51 and 1964-5 respectively) are provided therein. It should be emphasized, however, that conditions in the lakes have changed considerably since the collections reported upon were taken. As well as the diversion of the Umfolosi River, the channel has been dredged to facilitate water movement and faunal migration, and the mouth has been stabilised by breakwaters. Despite these efforts to improve conditions, salinity in the system in recent years has risen at times to well in excess of 100‰. This has undoubtedly affected the fauna but the nature of such effects will only be determined by further sampling.

At the time of sampling eight species of amphipod were found. *Afrochiltonia capensis* and *Orchestia rectipalma* were common in areas of low salinity where rivers enter the system, while *Grandidierella bonnierii* and *Melita zeylanica* appeared tolerant of conditions of salinity from 0-50‰ and more. *Orchestia ancheidos* was found along the driftline throughout the system. Also recorded were

Corophium triaenonyx, found locally throughout the lakes, *Ampelisca anisuropha* from South Lake and *Eriopisa chilensis* from mangroves near the mouth.

St. Lucia station data

<i>Catalogue no.</i>	<i>Date</i>	<i>Location</i>
STL 11	4/7/48	Stony shore, Charters Creek
STL 18	4/7/48	Amongst <i>Zostera</i> , Charters Creek
STL 52	9/7/48	Mouth of estuary, shore collection
STL 67	12/7/48	Drift line near Charters Creek
STL 73	12/7/48	Decaying <i>Zostera</i> near Charters Creek
STL 77	15/7/48	Black mud, shore near Charters Creek
STL 89	19/7/48	River mouth, False Bay
STL 101	3/7/48	Near Charters Creek, plankton haul
STL 102	19/7/48	Hluhluwe River
STL 135	6/7/49	Amongst <i>Zostera</i> , Charters Creek
STL 148	8/7/49	Sandy shore, Charters Creek
STL 171	11/7/49	Sandy beach, mouth of estuary
STL 178	19/7/49	Sandy stones, False Bay
STL 188	20/7/49	Plankton haul, False Bay
STL 193	7/2/49	Mangrove swamps near mouth
STL 204	21/1/51	Stomach of fish, Charters Creek
STL 223	20/1/51	Stomach of fish, Charters Creek
STL 232	3/7/64	Seine netting, opposite Charters Creek
STL 243	1/7/64	River mouth, channel
STL 251	24/6/64	South Lake
STL 252	24/6/64	South Lake
STL 270	5/7/64	Rocky shore, South Lake
STL 274	26/6/64	Mangrove swamps above bridge
STL 296	10/1/65	Seine netting above bridge
STL 299	11/1/65	Shore collection, channel
STL 304	12/1/65	Shore collection, channel
STL 309	14/1/65	Seine, North Lake
STL 312	15/1/65	Seine, northern False Bay
STL 317	16/1/65	Shore collections, southern False Bay
STL 318	16/1/65	Shore collection, western False Bay
STL 337	23/1/65	Shore collection, North Lake
STL 339	24/1/65	Charters Creek, seine
STL 342	25/1/65	Shore stations, South Lake
STL 343	25/1/65	Charters Creek
STL 344	25/1/65	Charters Creek

(c) *Richard's Bay* (RHB)

Full details of the physical and biotic features of the area are to be found in Millard & Harrison (1954), but a brief summary is given here for the sake of convenience. Richard's Bay is a subtropical estuary situated 28°48'S/32°05'E. The estuary receives several sizeable rivers and is about 40 sq. km in area, consisting of a large triangular shallow lake opening to the sea through a narrow mouth. The body of the lake averages about 1 m depth but has a deeper perimeter. The bottom is mostly soft mud with a good growth of *Zostera* and the banks are generally marshy with occasional areas of mangrove. The channel flows from the north-east corner of the lake, its bottom changing from mud to sand as it approaches the sea. An hotel is situated on the north bank of the channel, while in its centre there is a small island known as Pelican Island.

In parts the channel may be 5 m deep.

Salinity in the main lake usually lies between 18–24‰, varying according to season. Near the river mouths the salinity decreases to zero, while it increases to that of sea water along the length of the channel.

A series of sampling expeditions to the lake between 1948 and 1951 by teams from the University of Cape Town revealed seven species of amphipod. *Grandidierella bonnieri* was abundant amongst the rich fauna of the *Zostera* beds, *Gitanopsis pusilla* and *Melita zeylanica* being found in lesser numbers in the same habitat. Around the shore of the system *Orchestia ancheidos* was common while *Eriopisa chilensis* was recorded in the mangroves and marshes. *Afrochiltonia capensis* and *Orchestia rectipalma* were to be found in areas of low salinity where rivers flowed into the lake.

Richard's Bay station data

<i>Catalogue no.</i>	<i>Date</i>	<i>Location</i>
RHB 5	21/7/48	Muddy bank opposite hotel
RHB 38	—/2/49	Sandy beach near mouth
RHB 39	26/1/49	Muddy shore, Pelican Island.
RHB 40	24/1/49	Amongst <i>Zostera</i> off Pelican Island
RHB 84	16/7/49	Trawl in <i>Zostera</i> bed
RHB 86	16/7/49	Netting in <i>Zostera</i> bed
RHB 93	17/7/49	Sandy beach below hotel
RHB 109	30/1/49	Muddy sand near mouth
RHB 113	25/1/51	Netting in <i>Zostera</i> , Pelican Island
RHB 114	25/1/51	Netting in shallows of channel
RHB 124	25/1/51	Netting in reeds at river mouth
RHB 127	26/1/51	Netting in mangroves near mouth
RHB 129	26/1/51	Hand-netting at river mouth
RHB 132	26/1/51	Sievings from <i>Zostera</i> near mouth

(d) *Durban Bay* (DBN)

A description of Durban Bay and its ecology may be found in Day & Morgans (1956). This landlocked bay has been extensively developed to form one of the largest harbours in the Southern Hemisphere. The narrow entrance is guarded by a pier to the north and a breakwater to the south. From the entrance the bay extends for about 6 km inland having a maximum width of about 4 km. The north, and much of the south bank, have been developed as a harbour, but at the time of sampling there were areas of mangrove to the south-west and large central sandbanks which were relatively undisturbed.

Two small polluted rivers flow into the bay but they do not significantly lower the salinity or affect tidal flow in the bay as a whole. Surface temperatures in the system vary between 20–25°C while currents and wave action are slight except in the entrance.

Durban Bay was visited on four occasions between 1950 and 1952 by zoologists from the University of Cape Town. The teams collected for about two weeks on each occasion, netting and dredging in deeper waters and digging or hand collecting intertidally.

Fifteen species of amphipod are represented in the collections. These

predominantly consist of hard-substrate types such as *Caprella equilibra*, *Stenothoe valida*, *Podocerus brasiliensis*, *Elasmopus pecteniscrus* and *Erichthonius brasiliensis*, which, to a large extent, inhabit artificial structures in the bay. Only five of the species were recorded from soft substrates and none of these were common. Although the muddy bottoms of the channels were sampled, no amphipods were recorded.

It is evident from these results that the fauna of the bay has been radically altered by human factors. Dredging and pollution of the channels have destroyed the benthic fauna of these areas while the intertidal sand flats have also been adversely affected by oil spillage, bait collecting and the like. The construction of wharfs has compressed much of the shoreline into vertical faces which lack the variety of niches found naturally, although favouring the proliferation of certain species.

Collection stations in the bay are denoted by the symbol DBN, those stations from which amphipods were recovered are listed below.

Durban Bay station data

<i>Catalogue no.</i>	<i>Date</i>	<i>Location</i>
DBN 2	7/7/50	Scraped from floating jetty
DBN 44	17/7/50	Amongst shelly sand, edge of channel
DBN 50	18/7/50	From sponge on muddy sand, centre banks
DBN 52	18/7/50	Netting in main channel
DBN 62	20/7/50	Collection from stones at culvert entrances
DBN 77	16/7/50	From <i>Zostera</i> , western shore
DBN 79	22/7/50	Sandy rocks, southern shore
DBN 131	15/1/51	Scrapings from ships hulls
DBN 143	9/1/51	Among algae, North Pier
DBN 158	30/9/51	Sand and drain pipes, southern shore
DBN 165	30/9/51	Intertidal rocks, southern shore
DBN 176	1/10/51	Hard objects at low tide, centre banks
DBN 192	2/10/51	Solid objects on causeway
DBN 199	3/10/51	From rocks, North Pier
DBN 201	3/10/51	From rocks, North Pier
DBN 241	23/4/52	From loose rocks, harbour entrance
DBN 251	24/4/52	Scrapings from buoy, mid channel
DBN 264	25/4/52	Surface of centre banks at low tide
DBN 271	26/4/52	Balanoid zone of pier
DBN 322	28/4/52	Concrete wall, south bank
DBN 371	30/4/52	Concrete wall, harbour entrance
DBN 373	30/4/52	Stones, harbour entrance
DBN 379	1/5/52	Scrapings from hull of launch
DBN 396	24/4/52	Scrapings from ship's hull
DBN 404	23/4/52	From buoy in channel.

(e) *Estuaries in the Umkomaas area (UMK)*

The samples in this series were collected from small estuaries between Durban and Umkomaas. The fast flowing muddy Umkomaas river proved devoid of amphipods while several species were found in the adjoining relatively clear estuaries of the Umgababa, Umzimbazi, Amalanga and Isipingo Rivers.

These rivers had estuaries typical of the area in that they are closed most of the year, breaking through to the sea during summer. Typical amphipods found under these conditions are *Afrochiltonia capensis* and *Orchestia rectipalma*,

found in conditions of low salinity, and *Melita zeylanica*, *Corophium triaenonyx*, *Grandidierella bonnieri* and *Grandidierella lignorum*, found nearer the mouths. *Orchestia ancheidos* is to be found along the banks of these estuaries.

UMK station data

<i>Catalogue no.</i>	<i>Date</i>	<i>Location</i>
UMK 18	29/1/50	Muddy sand near mouth, Umzimbazi River
UMK 19	29/1/50	Stones near mouth, Umzimbazi River
UMK 23	30/1/50	Amongst <i>Zostera</i> near mouth, Umzimbazi River
UMK 24	30/1/50	Shore collection, Umgababa River
UMK 25	30/1/50	Netting 1 km from mouth, Umgababa River
UMK 26	30/1/50	Collection from stones, Umgababa River
UMK 27	30/1/50	<i>Zostera</i> bed, Umgababa River
UMK 29	19/7/47	Grass around mouth, Amalanga River
UMK 33	19/7/50	Sandy bottom of Isipingo River
UMK 35	7/7/46	Umzimbazi River lagoon

(f) *Estuaries near Port Shepstone (SHP)*

Collections from the Umzimkulu, Umtentwini and Uvongo River estuaries are incorporated in this series. The clear sandy Uvongo lagoon did not reveal any amphipods but in the rich muddy Umzimkulu estuary *Grandidierella lignorum* was common. *Orchestia ancheidos* was found commonly around the banks of the Umtentwini.

SHP station data

<i>Catalogue no.</i>	<i>Date</i>	<i>Location</i>
SHP 2	22/1/50	Muddy rocks, mouth of Umzimkulu River
SHP 5	22/1/50	Grass on bank of Umtentwini River

(g) *Estuaries near Port Edward (EDW)*

During a brief visit to the Umtamvuna River estuary, 3 km from Port Edward, two species of amphipod were recorded. These were *Orchestia rectipalma* and *Afrochiltonia capensis*, which were both found along the driftline near the mouth of the estuary.

SYSTEMATICS

The systematic text is presented in alphabetical order of families, genera within each family, and then of species within each genus. Taxonomy follows J. L. Barnard (1969, 1970a) for the Gammaridea, and McCain (1970) for the Caprellidea. World species lists of these groups may be found in J. L. Barnard (1958), and McCain & Steinberg (1970) respectively.

Samples in the collections of the University of Cape Town are labelled according to a catalogue—sample—species code. Thus all samples from a particular area are denoted by a letter code, usually a triplet suggesting the name of the area covered (e.g. RHB for Richard's Bay). The first sample in this series is RHB 1 and the species within that sample are labelled RHB 1A, RHB 1B etc. This system has the advantage of enabling species to be labelled before their identity is known. Where the number of individuals of a species

has been recorded this is given after the catalogue number in brackets. Occasionally only an index of abundance (A—abundant, C—common, P—present) was recorded, in which case this is provided instead.

All previous records of amphipods from Natal in the literature are also noted. The location of benthic samples was frequently given by these authors in a somewhat vague fashion (e.g. 'off Cape Natal'). In these cases I have given the location in terms of the latitude/longitude square in which the sample was taken, followed by the depth. Thus 28/32/100 m indicates a record from the latitude/longitude square 28°S/32°E at a depth of 100 m. The source of the record follows the code in brackets. In a few cases in K. H. Barnard's papers the material reported on was derived from University of Cape Town collections. In these cases duplication has been avoided by giving only the University code.

Analysis is restricted to species occurring in less than 1 000 m of water, species occurring below this depth being regarded as abyssal, rather than as members of the South African fauna. Terrestrial and truly fresh-water species are omitted while estuarine species and those dwelling on the strand are included. No attempt has been made to provide a full list of synonyms but the reader is referred to at least one description of each species, preference being given to those incorporating good figures or pertaining specifically to the southern African region. Where brief diagnoses are given these are intended to differentiate the species from others in that genus. Generic diagnoses may be found in J. L. Barnard (1969*b*) for gammaridean genera or via McCain & Steinberg (1970) for caprellid genera. Where no diagnoses are provided here they may be found in Parts 1 and 2 of this series.

Limbs of the pereon have been referred to throughout as gnathopods 1 and 2, followed by pereopods 1–5. This follows K. H. Barnard and J. L. Barnard, but it should be noted that many authors, including McCain, Ledoyer and Schellenberg number pereopods according to the pereon segments on which they occur (i.e. gnathopods 1 and 2 followed by pereopods 3–7).

Type-specimens of all new species have been placed in the South African Museum, Cape Town.

Suborder GAMMARIDEA

Family Ampeliscidae

Ampelisca anisuropa (Stebbing, 1908)

Byblis anisuropus Stebbing, 1908: 72, pl. 10. K. H. Barnard, 1955: 82, fig. 40b.

Records: NIWR/1/15B(1), NIWR/2/33C(2); NAD 39B(8), NAD 66T(2).

Diagnosis: Antenna 1 as long as peduncle of antenna 2; antenna 2 as long as body; anterior margin of head oblique, sinuous; two pairs of eyes, with corneal lenses; article 3 of pereopod 5 shorter than 4, article 4 slightly lobed posteriorly, 5 not notched anteriorly, distally lobed to embrace the narrow article 6,

7 minute; third pleonal epimeron postero-distally rounded; pleon segment 4 bearing a triangular dorsal carina.

Distribution: Endemic, Natal to west coast of South Africa.

Remarks: This species is one of three intermediate between *Ampelisca* and *Byblis*. Normally *Ampelisca* can be distinguished from *Byblis* by virtue of the longer telson, which is more than 50 per cent cleft, by the lack of setae on the anterior margin of article 2 of pereopod 5 near its junction with article 3, and by the lamellar article 6 and lanceolate article 7 of pereopod 5.

Ampelisca byblisoides (K. H. Barnard), *Ampelisca subantarctica* (Schellenberg) and *Byblis anisuropus* Stebbing display a cleft telson, sparse setation of article 2 of pereopod 5 and a narrow article 6 and minute article 7 of pereopod 5. Since two of the species have been assigned previously to *Ampelisca* [*A. subantarctica* was moved from *Byblis* by J. L. Barnard (1966)] the move proposed here of *B. anisuropus* to the genus *Ampelisca* will enable these two genera to be clearly distinguishable by the degree of division of the telson and by the density of setae on pereopod 5.

Ampelisca brachyceras Walker, 1904

Ampelisca brachyceras Walker, 1904: 252, pl. 2, fig. 13.

Records: NIWR/2/30G(2), NIWR/2/33H(1).

Distribution: Ceylon, southern Africa.

Ampelisca brevicornis (Costa, 1853)

Ampelisca brevicornis: Reid, 1951: 204-210, figs 9-15.

Records: NIWR/1/14C(1), NIWR/UM/M4A(1), NIWR/UM/P1A(1), NIWR/2/33B(3), NIWR/2/36E(8); NAD 27B(3), NAD 43D(1), NAD 61B(1), NAD 86P(1).

Distribution: Mediterranean, Atlantic, Indo-Pacific.

Ampelisca chiltoni Stebbing, 1888

Ampelisca chiltoni Stebbing, 1888: 1042, pl. 103. J. L. Barnard, 1961: 61, fig. 31.

Records: NIWR/1/27F(1); NAD 11T(1).

Diagnosis: Antenna 1 as long as peduncle of 2; antenna 2 as long as body; anterior margin of head almost transverse; two pairs of eyes, with corneal lenses; article 3 of pereopod 5 slightly shorter than 4, article 4 slightly lobed posteriorly, 5 notched anteriorly, not embracing 6, which is almost as wide as 5, 7 as long as 6; third pleonal epimeron with a small postero-distal tooth; pleon segment 4 not carinate.

Distribution: Indo-Pacific.

Ampelisca diadema (Costa, 1853)

Ampelisca diadema: K. H. Barnard, 1916: 133. Chevreux & Fage, 1925: 82, fig. 74.

Records: NIWR/1/6A(1), NIWR/1/14B(1), NIWR/1/15C(4), NIWR/UM/D3D, NIWR/UM/R3F(6), NIWR/UM/M2D(1), NIWR/UM/M3E(2), NIWR/2/27F(1), NIWR/2/33G(1), NIWR/2/13A(1), NIWR/2/14K(1), NIWR/2/17D(2), NIWR/2/21C(1), NIWR/2/23D(14); NAD 4X(3); 30/30/24 m (K. H. Barnard 1916).

Distribution: Cosmopolitan.

Ampelisca fusca Stebbing, 1888

Ampelisca fusca Stebbing, 1888: 1052, pl. 105.

Records: NIWR/2/36G(4).

Distribution: Endemic, Moçambique to South West Africa.

Ampelisca miops K. H. Barnard, 1916

Ampelisca miops K. H. Barnard, 1916: 134, pl. 26, fig. 6.

Records: NIWR/1/27E(1), NIWR/2/30J(1); 29/31/80 m (K. H. Barnard 1916).

Diagnosis: Antenna 1 slightly exceeding peduncle of 2; antenna 2 as long as body; anterior margin of head oblique; one pair of eyes with corneal lenses; article 3 of pereopod 5 twice as long as 4, article 4 not lobed posteriorly, 5 not notched anteriorly, slightly produced over 6 anteriorly, 6 wider and much longer than 5, 7 almost as long as 6; third pleonal epimeron postero-distally acute, bi-sinuate above; pleon segment 4 with an acute dorsal carina.

Distribution: Endemic to Natal, the above records being the only ones to date.

Ampelisca natalensis K. H. Barnard, 1916

Ampelisca natalensis K. H. Barnard, 1916: 137, pl. 26, fig. 7.

Records: 29/31/200 m, 30/30/48 m (K. H. Barnard 1916).

Diagnosis: Antenna 1 considerably longer than peduncle of 2; antenna 2 shorter than body; anterior margin of head oblique; two pairs of eyes with corneal lenses; article 3 of pereopod 5 equal to 4 plus 5, 4 not lobed posteriorly, 5 not notched, not embracing 6 which is equal to 3; 7 almost as long as 6; third pleonal epimeron postero-distally slightly produced; pleon segment 4 with a slight dorsal keel.

Distribution: Endemic to Natal.

Ampelisca palmata K. H. Barnard, 1916

Ampelisca palmata K. H. Barnard, 1916: 136, pl. 28, figs 30-31.

Records: NIWR/2/24A(1), NIWR/2/36F(4); 29/31/200 m (K. H. Barnard 1916).

Distribution: Southern and west Africa.

Ampelisca spinimana Chevreux, 1887

Ampelisca spinimana: Chevreux & Fage, 1925: 81, fig. 73.

Records: NAD 27A(22), NAD 49S(1), NAD 56C(7), NAD 61C(2), NAD 66U(2); NA 189W(1).

Distribution: Eastern Atlantic, extending to Natal.

Byblis gaimardi (Kröyer, 1846)

Byblis gaimardi: Mills, 1971: 367-370, figs 6A, 7.

Records: NIWR/A/3A(1), NIWR/1/14A(2), NIWR/1/15A(2), NIWR/1/26B(2), NIWR/1/27C(3), NIWR/UM/M2C(1), NIWR/UM/M3B(3), NIWR 2/27A(5), NIWR/2/30H(1), NIWR/2/36D(9), NIWR/2/23B(5); 29/31/200 m (K. H. Barnard 1916).

Diagnosis: Front margin of head concave, corneal lenses present; article 4 of pereopod 5 more than twice as long as article 3; articles 4 and 5 parallel sided, 5 not embracing 6 distally, 6 almost as long as 5; uropod 3 barely exceeding 1 and 2; telson 20 per cent cleft.

Distribution: North Atlantic, ? Pacific, Arctic, South Africa.

Triodos insignis K. H. Barnard, 1916

Triodos insignis K. H. Barnard, 1916: 140, pl. 26, figs 8-10.

Records: 29/31/200 m (K. H. Barnard 1916).

Diagnosis: As this genus is monotypic the characters of the genus diagnose the species. One pair of eyes, antero-ventral corner of head produced; flagellum of antenna 2 of about 28 articles; article 2 of pereopod 5 greatly expanded distally, posterior edge oblique, articles 3 and 4 equal, together equal to 5, 6 narrow, 7 spiniform; pleon with segments 4 and 5 keeled, keels bearing tufts of setae; telson ovate, cleft nearly to base.

Distribution: The above record is the only one to date.

Family **Amphilochidae***Amphilochus neapolitanus* Della Valle, 1893

Amphilochus neapolitanus: J. L. Barnard, 1962b: 126, fig. 3.

Records: DBN 50D.

Diagnosis: Eyes round or slightly oval, fairly small; antenna 1 extending beyond peduncle of antenna 2; coxa 1 quadrate; article 5 of gnathopod 1 extending 75 per cent of way along hind margin of 6; gnathopod 2 larger than 1, article 5 produced along entire hind margin of 6, palm transverse; telson much shorter than peduncle of uropod 3.

Distribution: Cosmopolitan in tropical and temperate seas.

Cyproidea ornata (Haswell, 1880)

Cyproidea ornata: J. L. Barnard, 1972: 21, figs 4-5.

Records: NIWR/2/24G(1), NIWR/2/30Q(1), NIWR/2/36M(1); Port Shepstone (K. H. Barnard 1925).

Distribution: Indo-Pacific, extending to South West Africa.

Gitanopsis pusilla K. H. Barnard, 1916

Gitanopsis pusilla K. H. Barnard, 1916: 144.

Records: NIWR/1/5B(1), NIWR/1/9A(1), NIWR/1/27M(3), NIWR/2/24J(1), NIWR/2/27K(1), NIWR/2/30N(1), NIWR/2/35B(1), NIWR/2/36L(5), NIWR/UM/M1C(1); RHB 40B(2).

Distribution: Southern Africa, southern ocean islands.

Family **Ampithoidae***Ampithoe africana* K. H. Barnard, 1925

Ampithoe africana K. H. Barnard, 1925: 361.

Records: DBN 143D(1), DBN 241V(1), DBN 271D(1), DBN 322F(1); NA 244J(5).

Diagnosis: Antenna 2 strongly setose; article 2 of gnathopods 1 and 2 lobed, article 6 of gnathopod 1 ovate, palm oblique, sinuate; article 6 of gnathopod 2 ovate-oblong, palm oblique, straight or slightly concave, defining angle obtuse with a short stout spine, dactyl serrulate; article 2 of pereopods 1 and 2 not strongly expanded, twice as long as broad.

Distribution: Endemic, Knysna to Durban.

Cymadusa filosa Savigny, 1818

Cymadusa australis: K. H. Barnard, 1940: 480.

Cymadusa filosa: J. L. Barnard, 1955: 29, fig. 15.

Records: G 13D, G 15D.

Distribution: Circumtropical.

Exampithoe natalensis K. H. Barnard, 1925

Exampithoe natalensis K. H. Barnard, 1925: 363, pl. 34, figs 16, 17.

Records: Port Shepstone (K. H. Barnard 1925).

Diagnosis: This genus is monotypic so the characters of the genus identify the species. Antenna 1 without accessory flagellum; mandible with slender palp, molar greatly reduced; gnathopod 1 stouter but shorter than 2; article 6 of pereopods 3-5 apically expanded; outer ramus of uropod 3 with two hooks.

Distribution: The above record is the only one to date.

Family **Aoridae***Aora typica* Kröyer, 1845

Aora typica: Ledoyer, 1967: 131, fig. 15.

Records: Durban (K. H. Barnard 1916).

Distribution: Cosmopolitan.

Lemboides acanthiger K. H. Barnard, 1916

Lemboides acanthiger K. H. Barnard, 1916: 239, pl. 28, figs 7-8.

Records: NAD 27C(1), NAD 56E(2); 29/31/110 m (K. H. Barnard 1916).

Diagnosis: Ventral surface of pereon segments 3 and 4 with large forwardly-directed curved spines, smaller spines on segments 5-7; palm of gnathopod 1 oblique, defined by a large acute tooth, dactyl nearly twice as long as palm, smooth; palm of gnathopod 2 smoothly concave.

Distribution: Endemic; Natal to False Bay.

Lembos hypacanthus K. H. Barnard, 1916

Lembos hypacanthus K. H. Barnard, 1916: 237, pl. 28, figs 5-6.

Records: NAD 43E(1).

Distribution: Endemic, Natal to South West Africa.

Microdeutopus thumbellinus n. sp.

Fig. 2

Description of male (3.5 mm): Head as long as first two pereon segments, ocular lobes short, acute, eyes large, oval, their centres dark but the peripheries colourless; (both antennae missing); primary cutting edge of mandible with four teeth, lacinia mobilis with five teeth, spine row of five spines, molar quadrate, triturative, palp short and stout, 3-articulate; maxilla 1 with 2-articulate palp exceeding outer plate, palp tipped by nine spines and three setae, outer plate with 10 terminal spines, inner plate tipped by a single seta; inner and outer plates of maxilla 2 subequal; maxilliped of normal structure, bearing 4-articulate palp.

Coxa 1 produced antero-distally into an acute point (Fig. 2A), ventral margin concave, remaining coxae rounded-quadrate, diminishing in size posteriorly; article 2 of gnathopod 1 expanding distally from a narrow base, article 5 greatly enlarged, its posterior margin distally produced into a single triangular tooth, an unusual large blunt process arises from the centre of the inner surface of the article (Fig. 2B), article 6 shorter and considerably narrower than 5, dactyl subequal to 6; gnathopod 2 subchelate, much smaller than 1, articles 5 and 6 subequal, dactyl slightly exceeding oblique undefined palp; (pereopods 1-5 missing); pereon segments lacking any ventral processes.

Pleonal epimera 1-3 postero-distally rounded; uropods extending equally; peduncle of uropod 1 (Fig. 2C) bearing four dorsal spines and a large terminal spine, inner ramus slightly the longer, rami strongly spinose dorsally and terminally; uropod 2 (Fig. 2D) similar to 1 but without a terminal peduncular spine; uropod 3 (Fig. 2E) with a single dorsal spine on the peduncle, rami subequal, spinose; telson quadrate, fleshy, a short thick spine and two setae at each distal apex.

Holotype: SAM A13222, male, 3.5 mm.

Type-locality: NIWR/UM/PIE, 15 September 1970; 29°59'S/31°03'E, depth 60 m.

Female: Similar to the male except for the structure of gnathopod 1 (Fig. 2H), which is like gnathopod 2, and the presence of brood pouches.

Relationships: Adults of this species are easily distinguished by virtue of the unusual projection arising from the inner surface of article 5 of gnathopod 1 male. In male specimens under 3 mm this process is less obvious (Fig. 2G), but specimens can still be identified by the lack of accessory teeth on article 5 of gnathopod 1, and by the relative size of article 5 and 6, which features are unusual for the genus. *Microdeutopus damnoniensis* (Bate) is probably the most closely related species but has rounded ocular lobes and smaller eyes, as well as lacking the process on article 5 of gnathopod 1.

Material: NIWR/UM/PIE(2), NIWR/UM/MIE(2), NIWR/2/21A(1), NIWR/2/24D(9), NIWR/2/30R(1), NIWR/2/36R(5).

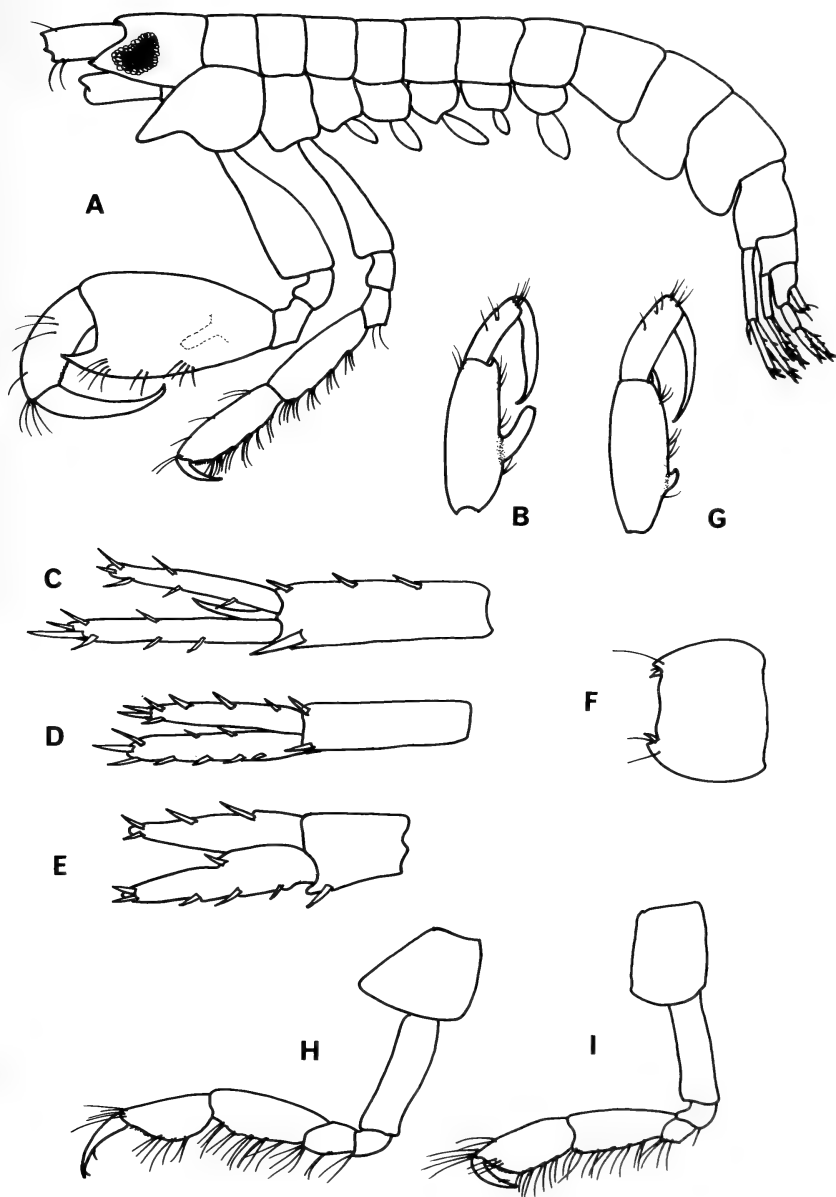


Fig. 2. *Microdeutopus thumbellinus* n. sp.

Male, 3,5 mm: A—lateral aspect; B—dorsal view of articles 5-7 of gnathopod 1; C, D, E—uropods 1, 2, 3; F—telson. Male, 3 mm: G—dorsal view of articles 5-7 of gnathopod 1. Female, 3 mm: H—gnathopod 1; I—gnathopod 2.

Family **Colomastigidae***Colomastix pusilla* Grube, 1864

Colomastix pusilla: J. L. Barnard, 1955: 39-42, fig. 20.

Records: NAD 7B(2).

Distribution: Cosmopolitan in tropical and temperate seas.

Family **Corophidae***Cerapus tubularis* Say, 1817

Cerapus tubularis: J. L. Barnard, 1962b: 61, figs 27-28.

Records: NIWR/2/27E(2), NIWR/2/28A(1), NIWR/2/30L(6); NAD 19C(3); NA 244K(1); 28/32/165 m (K. H. Barnard 1916 as *C. abditus*); 29/31/430 m (J. L. Barnard 1961).

Distribution: Cosmopolitan in warm and temperate seas.

Corophium acherusicum Costa, 1857

Corophium acherusicum: J. L. Barnard, 1971: 59, figs 17, 26.

Records: DBN 50C(P), DBN 131H(P), DBN 176V(2), DBN 251F(1), DBN 271C, DBN 396C(4); Durban Bay (K. H. Barnard 1916).

Distribution: Cosmopolitan in tropical and temperate seas.

Corophium triaenonyx Stebbing, 1904

Corophium triaenonyx Stebbing, 1904: 25, pl. 6A.

Records: STL 252G, STL 296V(3), STL 309G(70), STL 312H(2); UMK 18T(C), UMK 19V(C), UMK 23P(C), UMK 25E(P), UMK 26D(C), UMK 27P(C); Lake Sibayi (Bolt 1969).

Distribution: Mediterranean, Atlantic and Indian Oceans.

Erichthonius brasiliensis (Dana, 1853)

Erichthonius brasiliensis: J. L. Barnard, 1971: 61, fig. 17E.

Records: DBN 50B(P), DBN 131N(1), DBN 241U(C), DBN 251E(C), DBN 264H(P), DBN 396B(P); NA 243D(1).

Distribution: Cosmopolitan in tropical and temperate seas.

Grandidierella bonnieri Stebbing, 1908

Grandidierella bonnieri: Ledoyer, 1967: 137, fig. 28A.

Records: DBN 44M, DBN 50A(P), DBN 52R, DBN 77B(4), DBN 165P(1); STL 89J(P), STL 101B, STL 188A, STL 204F, STL 223A(2), STL 312S(1);

RHB 5G(A), RHB 39A(1), RHB 40A(C), RHB 84D(A), RHB 86L, RHB 109A(1), RHB 113J(C), RHB 114C(1); UMK 11E(P), UMK 23R(C), UMK 27M(C); Umlalazi estuary (Hill 1966).

Distribution: Caribbean, Atlantic and Indian Oceans.

Grandidierella lignorum K. H. Barnard, 1935

Grandidierella lignorum K. H. Barnard, 1935: 300, fig. 14.

Records: UMK 18S(A), UMK 23S(P), UMK 25D(P), UMK 26F(P), UMK 27C(P), UMK 33D(2); SHP 2A(C); Lake Sibayi (Bolt 1969).

Diagnosis: Pereon segments of male without ventral processes; coxae 1 and 2 sharply pointed antero-distally; article 5 of gnathopod 1 ovoid, a pointed process on lower distal corner, another on distal margin and a third on hind margin.

Distribution: Endemic to brack waters on east coast of South Africa.

Siphonoecetes dellavallei Stebbing, 1893

Siphonoecetes dellavallei: Chevreux & Fage, 1925: 361, fig. 369.

Records: NIWR/1/26D(3), NIWR/1/27N(1), NIWR/2/21D(1), NIWR/2/23F(3).

Distribution: Mediterranean, southern Africa.

Siphonoecetes orientalis Walker, 1904

Siphonoecetes orientalis Walker, 1904: 294, pl. 7, fig. 49. K. H. Barnard, 1916: 270.

Records: NAD 86Q(9); 29/31/200 m (K. H. Barnard 1916).

Distribution: Tropical Indo-Pacific.

Unciolella spinosa n. sp.

Fig. 3

Description of male (7 mm): Head as long as first two pereon segments, eyes fairly large, round, colourless, head produced into a small lobe immediately below eye; antenna 1 as long as pereon plus pleon, articles 1 and 3 subequal, each 80 per cent as long as article 2, flagellum shorter than peduncle, 9-articulate, accessory flagellum of two long articles and one small article; (antenna 2 missing); mandible (Fig. 3B) with triturative molar and 3-articulate palp, spine row of eight strong spines, articles 2 and 3 of palp slightly longer than article 1, article 3 with an oblique row of medial plumose setae and a row of about 25 setae terminally; inner plate of maxilla 1 tipped by a single seta, outer plate bearing eight serrate spines, palp bi-articulate, terminally bearing three setae and five spine teeth; inner plate of maxilliped (Fig. 3D) with a row of

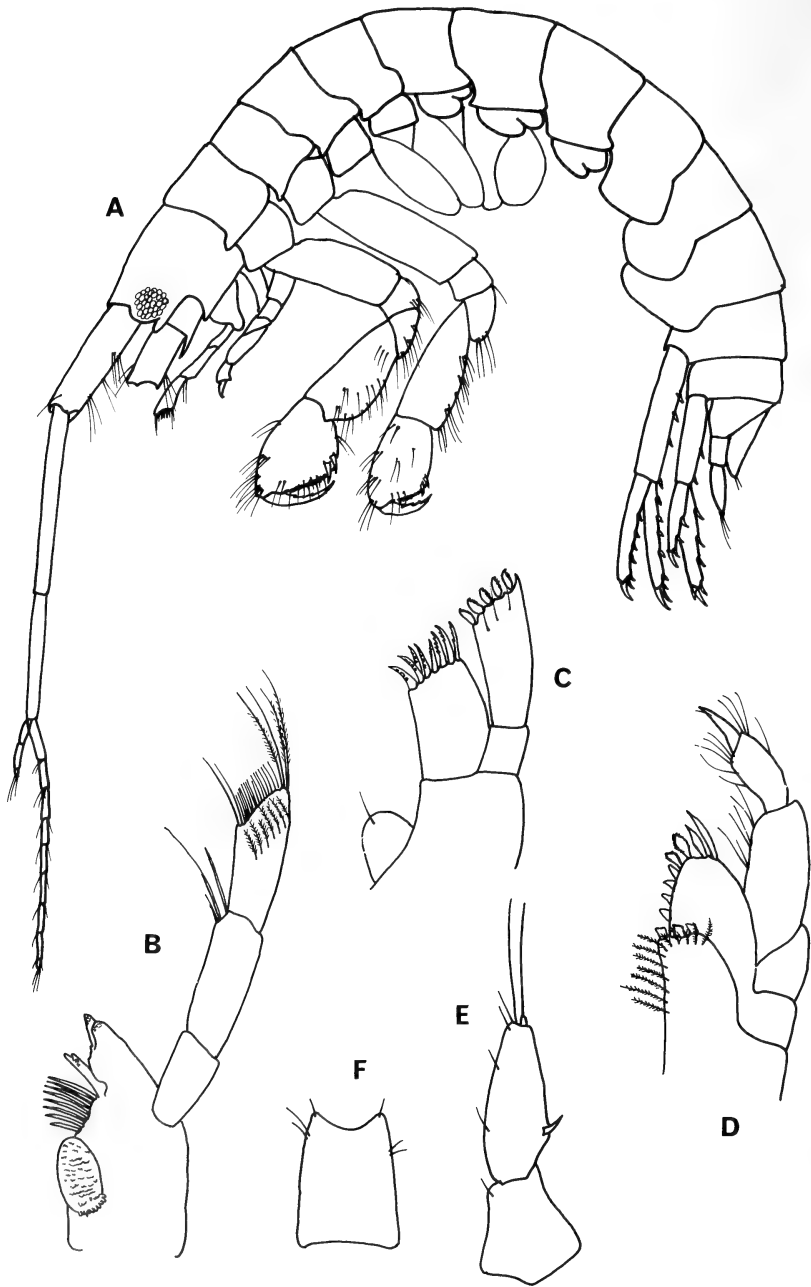


Fig. 3. *Unciolella spinosa* n. sp.
Male, 7 mm: A—lateral aspect; B—mandible; C—maxilla 1; D—maxilliped; E—uropod 3;
F—telson.

lateral plumose setae and three terminal spine teeth, outer plate marginally bearing eight successively longer spine teeth, palp 4-articulate.

Surface of body porcelainous with scattered pits and furrows but these less marked than in *U. foveolata* K. H. Barnard, 1955; coxae 1-4 quadrate, remaining coxae rounded; gnathopod 1 slightly larger than 2, article 2 expanding markedly from its base, article 5 slightly longer than 6, palm oblique, minutely pectinate, defined by two very large spines, dactyl cut into 3 teeth, equal to palm; gnathopod 2 resembling 1 but slightly smaller and more elongate, palm pectinate, defined by 2 spines, dactyl serrate; (pereiopods all missing); pereon segments 3-5 each with a single mid-ventral forwardly directed spine, spines becoming smaller posteriorly.

Pleonal epimera 1-3 smoothly rounded; uropod 1 large (Fig. 3A), peduncle with four dorsal spines, rami equal, each with four dorsal and 3-4 terminal spines; uropod 2 extending as far as 1, exceeding uropod 3 by nearly the whole length of the rami, outer ramus 70 per cent as long as inner, bearing two dorsal and two terminal spines; uropod 3 uniramous, much shorter than 1 and 2, peduncle medially expanded (Fig. 3E), bearing single seta, ramus 1.5 times peduncle, bearing a single lateral spine, 2-3 terminal setae and a minute second article which is hardly more than an expanded base to the single large seta it bears; telson large, fleshy, distally emarginate with a single seta at each apex and 2 marginal setae on each side.

Holotype: SAM A13217, male 7 mm.

Type-locality: NIWR/1/27P, 15 May 1972, 30°47'S/30°33'E, depth 58 m.

Female: Similar to the male except for the possession of broad plates and the absence of mid-ventral spines on the pereon segments; ovigerous at 5 mm.

Relationships: There are only two other species in this genus, *U. foveolata* K. H. Barnard, 1955 and *U. lunula* Chevreux, 1910. The present species can be distinguished from these by the enlarged uropods 1 and 2, which in the other two species barely exceed uropod 3; by the presence of mid-ventral spines on segments 3-5 and by the 3-articulate accessory flagellum (this is uni-articulate in *U. lunula* and 4-5 articulate in *U. foveolata*).

Remarks: It is characteristic of this species, and of *U. foveolata* to which it is obviously closely related, to autotomize its appendages when preserved. Animals almost invariably lack antennae and pereiopods, although the gnathopods are seldom lost. Over 100 individuals of the present species are represented in the collections of the University of Cape Town, and of these only one, the holotype, possesses a first antenna enabling it to be described.

The placement of this genus in Corophiidae as opposed to Isaeidae or Aoridae, to which it could equally well belong, underlines the impossibility of distinguishing these three families and the necessity for their fusion.

Material: NIWR/1/13B(1), NIWR/1/27P(2), NIWR/UM/PIC(1), NIWR/UM/P5A(2), NIWR/2/21B(2), NIWR/2/24C(18), NIWR/2/27D(2), NIWR/2/30F(1), NIWR/2/36P(9).

Family **Dexaminidae***Atylus granulatus* (Walker, 1904)

Atylus granulatus: Ledoyer, 1967: 127, fig. 8.

Records: NIWR/2/36K(1); 30/30/200 m, 29/32/50 m (K. H. Barnard 1916).

Diagnosis: K. H. Barnard's (1916) specimens agree with Walker's (1904) brief description except that pleon segment 1 as well as 2 and 3 show carinae produced into small acute teeth posteriorly; the urosomal carinae are much larger than figured by Ledoyer (1967); urosome segment 1 has a small setiferous notch followed by a deep depression and a hoodlike arched process, segment 2 plus 3 smoothly arched distally; article 2 of pereopod 3 postero-distally produced into a strong curved process extending beyond the tip of article 3.

Distribution: Indian Ocean.

Polycheria atolli Walker, 1905

Polycheria atolli: Ledoyer, 1967: 131, fig. 13A.

Records: NIWR/1/14L(1); D 96A; NAD 16P(2).

Distribution: Southern oceans, extending into tropical Indian Ocean.

Family **Eusiridae***Eusiroides monoculodes* (Haswell, 1880)

Eusiroides monoculodes: J. L. Barnard, 1964: 221, fig. 1.

Records: NAD 4W(2), NAD 81J(2), NAD 191G(2); 30/30/24 m, 29/31/100 m (K. H. Barnard 1916).

Distribution: Cosmopolitan.

Paramoera capensis (Dana, 1853)

Paramoera capensis: K. H. Barnard, 1916: 183-186.

Paramoera schizurus Stebbing, 1918: 66, pl. 10.

Records: D 261; M 19F; Durban (Stebbing 1918); Port Shepstone (K. H. Barnard 1940).

Distribution: Atlantic, Indo-Pacific.

Rhachotropis grimaldi Chevreux, 1887

Rhachotropis grimaldi: K. H. Barnard, 1916: 179.

Records: 29/3/800 m (K. H. Barnard 1916).

Diagnosis: Pereon not carinate but segment 7 in male with a small median tooth; pleon segments 1-3 dorsally tricarinate, all the carinae ending in acute

scarcely-upturned teeth, pleon segment 4 with a single median carina; article 2 of pereopod 5 with serrate hind margin, postero-distal angle rounded; pleonal epimera 2 and 3 posteriorly serrate.

Distribution: Atlantic, extending to Natal.

Family **Gammaridae**

***Ceradocus natalensis* n. sp.**

Fig. 4

Description of male (10 mm): Head slightly shorter than two pereon segments, a pronounced slit below the eye, which is large and dark; antenna 1 reaching end of pereon, articles 1 and 2 subequal, 3 short, flagellum of 20–25 articles, accessory flagellum of about nine articles; antenna 2 slightly shorter than antenna 1, article 2 produced ventrally to tip of article 3; article 1 of mandibular palp with inner margin distally produced, article 3 slightly less than half length of article 2 (Fig. 4D), inner plate of maxilla 1 densely setose, outer plate armed with forked and serrate spines, palp with about 11 apical setae; inner plate of maxilla 2 densely setose medially and terminally; outer plate of maxilliped armed with serrate spines.

Coxa 1 acutely produced anteriorly, lower margin with a few fine setae; article 2 of gnathopod 1 expanded just below its origin, articles 5 and 6 subequal and densely setose posteriorly; palm oblique, setose, not defined; dactyl equal to palm (Fig. 4A); gnathopod 2 differing on the two sides, that of the left side very large, article 2 anteriorly keeled, article 5 cup-shaped, 6 very large; palm transverse with a strong defining tooth, a few irregular crenulations and then a square topped tooth and a step near the finger hinge; dactyl as long as palm, abruptly constricted near its origin to fit the step in palm; gnathopod 2 of right side much smaller, article 6 less than twice length of 5, palm oblique, convex; dactyl equal to palm, not constricted; pereopod 1 slightly longer than 2 (pereopods 3–5 missing).

Pleon segments 1–3 with posterior margins dorsally serrate; segments 1 and 2 with 6 teeth on each side, the central pair the smallest and the second pair the largest; third pleon segment also with 6 pairs of teeth dorsally, the most lateral pair the largest; first pleonal epimeron with a tooth at postero-inferior corner and a much smaller one above and below it, an oblique ridge runs across the epimeron to the corner tooth; second pleonal epimeron similar but with two teeth on posterior margin; third pleonal epimeron without oblique ridge, three teeth on lower margin, a larger one at postero-inferior corner, and five along the posterior margin; pleon segment 4 with a flat-lying mid-dorsal tooth flanked by a pair of much larger upstanding teeth; pleon segment 5 smooth mid-dorsally, with three pairs of small lateral teeth; uropod 1 extending slightly beyond uropod 2, rami equal, subequal to peduncle; outer ramus of uropod 2 slightly shorter than inner; uropod 3 (Fig. 4F) extending well beyond 1 and 2,

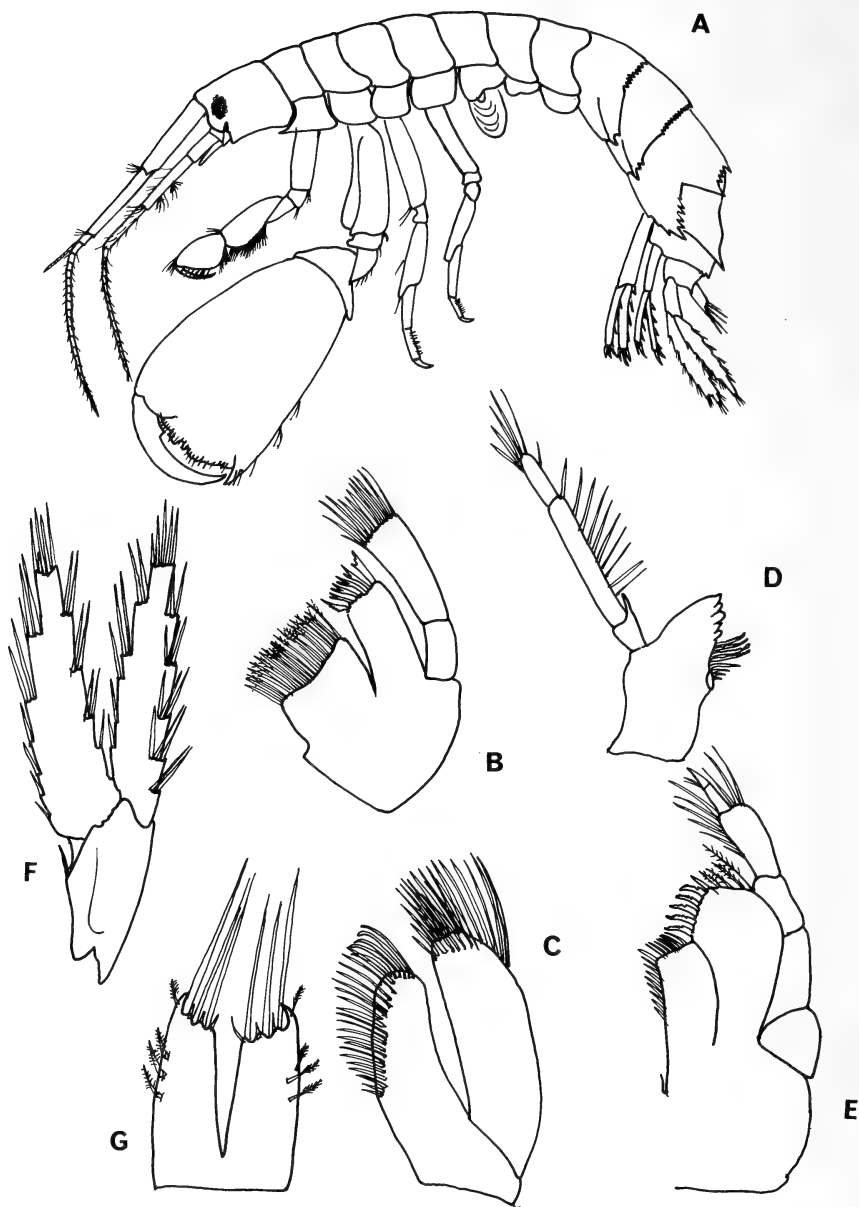


Fig. 4. *Ceradocus natalensis* n. sp.
Male, 10 mm: A—lateral aspect; B—maxilla 1; C—maxilla 2; D—mandible; E—maxilliped;
F—uropod 3; G—telson.

rami broad, subequal, heavily spinose; telson cleft almost to base, each lobe with four plumose setae on lateral margin and three long terminal spines, three small spines lying at bases of long spines. (Fig. 4G).

Holotype: SAM A13164, male 10 mm.

Type-locality: NAD 4N, 30°47'S/30°29'E, 17 May 1958, depth 44 m, substrate stones.

Relationships: The genus *Ceradocus* was revised by Sheard (1939). The present species falls into his subgenus *Denticeradocus* by virtue of its multi-dentate pleon segments. It can be distinguished from other species in the group by details of pleonal armature and structure of the telson, as well as by the shape of gnathopod 2. Closely related species include *Ceradocus chevreuxi* Sheard, which has five large spines on each lobe of the telson, and *C. hawaiiensis* J. L. Barnard which has two spines at each telsonic apex and a more strongly toothed second gnathopod.

Material: NAD 4N, two males.

Cerodocus rubromaculatus (Stimpson, 1885)

Cerodocus rubromaculatus: J. L. Barnard, 1972: 220, fig. 129.

Records: NIWR/1/27B(1), NIWR/UM/R3A(1); NAD 4T(4).

Distribution: Indo-Pacific, extending to South West Africa.

Elasmopus affinis Della Valle, 1893

Elasmopus affinis: Sars, 1895: 521, pl. 183.

Records: NAD 7A(1).

Distribution: Mediterranean, Atlantic, southern Indian Ocean.

Elasmopus japonicus Stephensen, 1932

Elasmopus japonicus Stephensen, 1932: 490, figs 1-2. Sivaprakasam, 1968: 278, figs 3-5.

Records: D 273; Durban (K. H. Barnard 1925 as *E. spinimanus*); Isipingo (K. H. Barnard 1940).

Distribution: Japan, India, southern Africa.

Elasmopus pecteniscus Bate, 1862

Elasmopus pecteniscus: J. L. Barnard, 1970b: 125, figs 73-74.

Records: DBN 2V, DBN 62G(C), DBN 79A, DBN 131G(C), DBN 158X(1), DBN 176U(3), DBN 192L(1), DBN 199V(C), DBN 201H(3), DBN 241T(C), DBN 251D(C), DBN 264L, DBN 396A(C), DBN 371E(1), DBN 379B(FC); G 15H; U 28F; M 19D; Durban (K. H. Barnard 1916).

Diagnosis: Eyes without black pigment; outer ramus of uropod 3 lacking article 2, inner ramus $\frac{2}{3}$ outer; telson of medium length, apices truncate, with 4–6 apical spines; gnathopod 2 male with hirsute, S-shaped, undefined palm, a small process distally and a ridge on inner proximal surface; dactyl simple, curved, longer than palm; article 2 of pereopod 4 male postero-distally excavate and serrate.

Distribution: Cosmopolitan in tropical and temperate seas.

Eriopisa chilensis (Chilton, 1921)

Niphargus chilensis Chilton, 1921: 531, fig. 4.

Records: RHB 127J(1); STL 193A(1).

Diagnosis: Eyes small, irregular; head without lateral cephalic notch; article 4 of gnathopod 1 produced posteriorly into a rounded lobe; palm of gnathopod 2 oblique, sinous, sub-equal to hind margin; articles 1 and 2 of outer ramus of uropod 3 subequal; pleonal epimera 1 and 2 not setose, third pleonal epimeron postero-distally quadrate, slightly produced; telson cleft to base, a single stout seta at apex of each lobe.

Distribution: India, east coast of South Africa.

Maera hamigera (Haswell, 1880)

Maera hamigera: K. H. Barnard, 1916: 196 pl. 27, figs 11–12. J. L. Barnard, 1965: 507, fig 16.

Records: NIWR/1/26G(1), NIWR/2/27J(1); 29/31/170 m (K. H. Barnard 1916).

Distribution: Indo-Pacific.

Maera inaequipēs Costa, 1851

Maera inaequipēs: J. L. Barnard, 1959: 25, pl. 5.

Records: NIWR/1/27L(2), NIWR/2/36J(1); NA 189X(12), NA 191F(3), NA 205K(1); M 19G.

Distribution: Cosmopolitan in tropical and temperate seas.

Mallacoota subcarinata (Haswell, 1880)

Maera subcarinata: K. H. Barnard, 1940: 460, fig. 26.

Mallacoota subcarinata: J. L. Barnard, 1972: 247, figs 144–145.

Records: D 117; NAD 16R(2); 'Natal' (K. H. Barnard 1940).

Distribution: Mediterranean, Indo-Pacific.

Remarks: J. L. Barnard (1972) has redefined the genus *Maera* such that species with paired dorsal carinae on pleon segment 4 are transferred to a new genus, *Mallacoota*. *M. subcarinata* is the only species from South Africa affected by this change.

Megaluropus namaquaeensis Schellenberg, 1953

Megaluropus namaquaeensis Schellenberg, 1953: 117, fig. 5.

Records: NIWR/UM/MiD(1).

Distribution: Endemic, Natal to South West Africa.

Melita appendiculata Say, 1818

Melita appendiculata: J. L. Barnard, 1970b: 161, figs 103-104.

Records: NAD 4L(180), NAD 56B(11), NAD 66S(1), NAD 81G(6); DBN 131L(1), DBN 396D(3); Durban, 29/31/54 m, 'Morewood Cove' 50 m (K. H. Barnard 1916 as *M. fresnelii*).

Distribution: Cosmopolitan.

Melita zeylanica Stebbing, 1904

Melita zeylanica: J. L. Barnard, 1972: 235, figs 139-141.

Records: DBN 373Y(2); STL 89H(C), STL 179E(P), STL 243U, STL 251L, STL 274G, STL 296U(10), STL 299Y(A), STL 302N(6), STL 305E(A), STL 312J(5), STL 318C(1), STL 337B(6), STL 339U(1), STL 343F(11), STL 343K(2), STL 344D(A); KOS 53G(P), KOS 62C(1), KOS 69F(19), KOS 74D(11), KOS 78F(18), KOS 82D(C), KOS 83N(3); RHB 5H(1), RHB 40C(2), RHB 84E, RHB 114C(1); UMK 18Q(C), UMK 19U(C), UMK 23Q(P), UMK 26E(C), UMK 27K(P), UMK 29B(P), UMK 35J; Umlalazi estuary (Hill 1966).

Distribution: Indo-Pacific region, in brack water.

Family **Haustoriidae***Platyschnopus herdmani* Walker, 1904

Platyschnopus capensis K. H. Barnard, 1925: 338, pl. 34, figs 13, 14.

Platyschnopus herdmani: Rabindranath, 1971: 521, figs 1, 2.

Records: NIWR/1/14J(1).

Diagnosis: Head longer than first four pereon segments, rostrum oblong, anteriorly rounded, encircled basally by weak spines, eyes present, subcutaneous, without ocelli; third pleonal epimeron postero-distally produced and upturned, pleon segment 3 with large medio-dorsal tooth and three lateral teeth on each side.

Distribution: India, South Africa.

Urothoe coxalis n. sp.

Fig. 5

Description of male (2.5 mm): Head equal to first three pereon segments, eyes small, round; antenna 1 with 4-articulate flagellum, accessory flagellum 2-articulate; antenna 2 about half length of body, flagellum of 15 rather broad articles; palp of maxilla 1 bi-articulate, tipped by three plumose setae, outer plate terminally bearing about eight strong spines, inner plate with a single terminal seta; mandible with large smooth molar and 3-articulate palp; articles 2 and 3 of palp subequal, twice length of 1; maxilliped with 4-articulate palp, article 2 densely setose medially, outer plate of maxilliped with four spine teeth on inner margin, inner plate terminally with three spines and four setae.

Coxa 1, narrow, evenly tapering to an acute point; coxa 2 slightly produced posteriorly and bearing three setae postero-distally; coxa 3 similar to 2; coxa 4 (Fig. 5G) hugely produced postero-distally into an acute upturned tooth, apex of the tooth extending beyond the posterior margin of coxa 5, coxa 5 bilobate, 6 and 7 rounded; gnathopod 1 (Fig. 5F) simple, article 5 expanded posteriorly, longer and twice as wide as 6; gnathopod 2 (Fig. 5E) slightly chelate, article 6 widening medially; pereiopods 1 and 2 with dactyl nodulose, article 6 strongly spinose postero-distally; pereiopod 3 (Fig. 5H, I) with article 2 quadrate, 4 with four antero-distal spines, 5 $1\frac{1}{2}$ times as wide as long, two groups of spines anteriorly, the proximal group of six spines and the distal group of five, also two groups of five and six spines on posterior margin, article 6 with three anterior fascicles of three, five and three spines and two posterior groups of four and three spines, dactyl broad, bearing two very strong spines in notches on its anterior border, below which it is minutely serrulate; pereiopods 4 and 5 not greatly expanded, posterior margin of article 2 bearing a few scattered plumose setae, dactyl bearing nodules on anterior margin.

First pleonal epimeron rounded postero-distally, second slightly produced, bearing long plumose setae on exterior surface, third pleonal epimeron strongly produced into an acute point above which it is bisinuate; uropods 1 and 2 with rami equal, unarmed; peduncle of uropod 3 (Fig. 5L) quadrate, rami broadly foliaceous, bearing long plumose setae marginally, outer ramus with a small article 2; telson (Fig. 5M) slightly exceeding peduncle of uropod 3, cleft to base, each lobe terminating in a single spine and a plumose seta.

Holotype: SAM A13211, male, 2.5 m.

Type-locality: NIWR/1/5D, 15 May 1972, 28°48'S/32°11'E, depth 16 m.

Female: Eyes of comparable size to those of the male, antenna 2 (Fig 5B) with 3-articulate flagellum, otherwise like male. The specimen figured measured 3 mm and was carrying four large ova.

Relationships: The greatly produced fourth coxa and the unusual dactyl of pereiopod 3 serve to diagnose this species. Only two other species, *Urothoe*

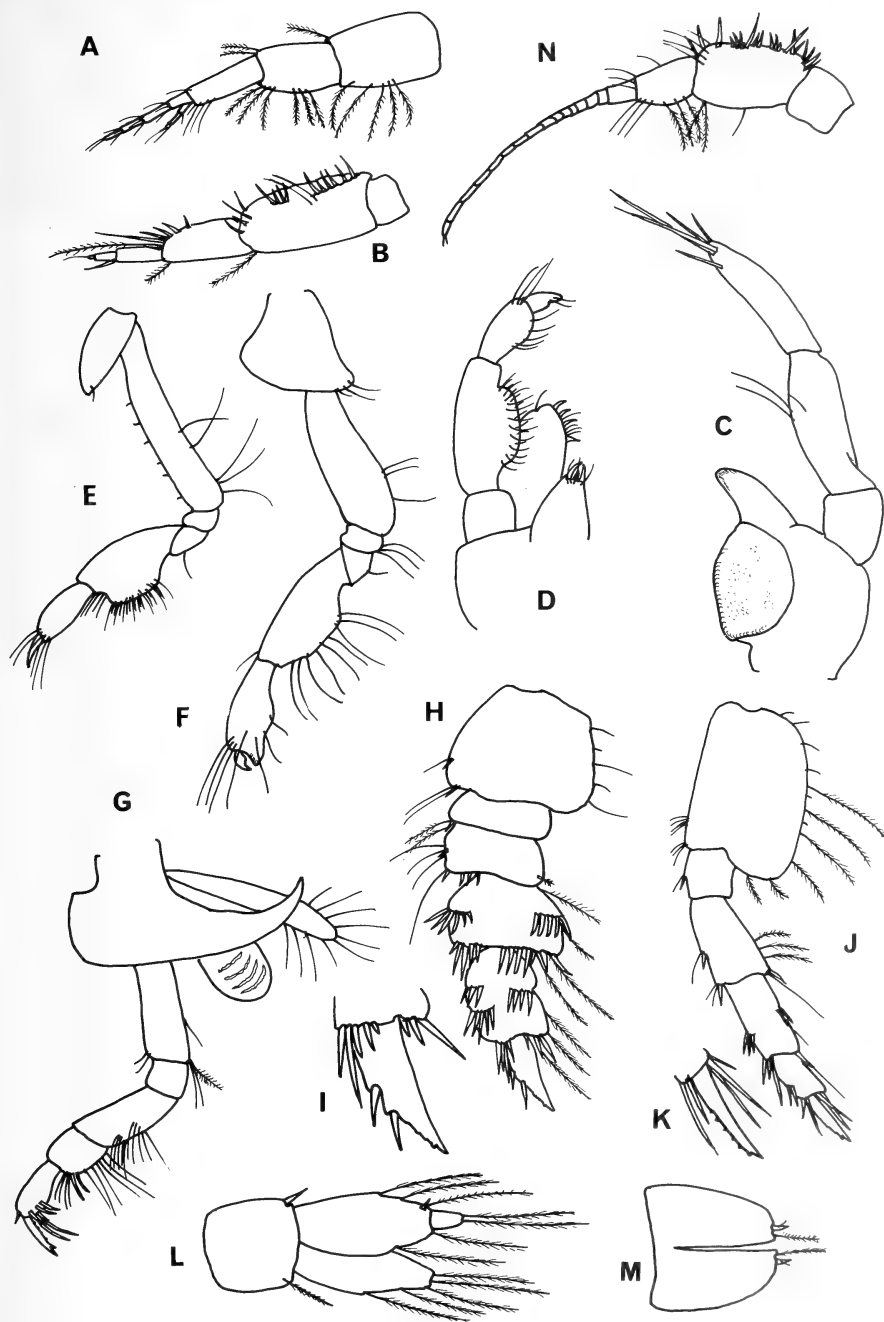


Fig. 5. *Urothoe coxalis*. n. sp.
 Female, 3 mm; A—antenna 1; B—antenna 2; C—mandible; D—maxilliped; E—gnathopod 1;
 F—gnathopod 2; G—pereopod 2; H—pereopod 3; I—dactyl of pereopod 3; J—pereopod 5;
 K—dactyl of pereopod 5; L—uropod 3; M—telson. Male, 2,5 mm: N—antenna 2.

grimaldii Chevreux, and *U. spinidigitus* Walker, have spinose dactyls on pereopod 3, but both bear more spines and lack the produced coxa 4 of *U. coxalis* n. sp.

Material: Single male and female from the type locality.

Urothoe elegans Bate, 1857

Urothoe elegans: Chevreux & Fage, 1925: 101, fig. 95.

Records: NIWR/1/14E(4), NIWR/1/27G(3), NIWR/UM/R3D(1), NIWR/UM/M3D(25), NIWR/2/23E(1), NIWR/2/27G(2), NIWR/2/30C(1), NIWR/2/32C(1), NIWR/2/33E(1).

Distribution: Atlantic and Indian Oceans.

Urothoe pinnata K. H. Barnard, 1955

Urothoe pinnata K. H. Barnard, 1955: 86, fig. 42.

Records: NIWR/2/20B(1).

Diagnosis: Antenna 1 of female with 6–8 articulate flagellum, accessory flagellum 5–6 articulate; article 6 of gnathopod 1 slightly expanded but simple; gnathopod 2 subchelate, palm rounded, dactyl equal to palm; pereopod 3 with article 2 oval, about $1\frac{1}{4}$ times as long as broad, article 5 twice as broad as long, 6 quadrate, dactyl narrow, minutely serrulate; article 2 of pereopod 5 about $1\frac{1}{2}$ times as long as broad.

Distribution: Endemic, Natal to False Bay.

Urothoe pulchella (Costa, 1853)

Urothoe pulchella: Chevreux & Fage, 1925: 99, fig 92. K. H. Barnard, 1955: 83, fig. 41A.

Records: NIWR/1/5C(1), NIWR/1/13C(3), NIWR/2/17C(5).

Diagnosis: Antenna 1 of female with 5-articulate flagellum and 3-articulate accessory flagellum; gnathopod 1 very weakly subchelate, article 6 expanding distally; gnathopod 2 distinctly subchelate, palm transverse; article 5 of pereopod 3 about $1\frac{1}{3}$ times as wide as long, dactyl slender, not cultriform, minutely pectinate.

Distribution: Mediterranean, Atlantic, South Africa.

Urothoe serrulidactylus K. H. Barnard, 1955

Urothoe serrulidactylus K. H. Barnard, 1955: 85, fig. 41C. Ledoyer, 1969: 185, fig. 3.

Records: KOS 82G(8).

Diagnosis: Antenna 1 of female with 6–8 articulate flagellum and 3–6 articulate accessory flagellum; gnathopod 1 simple, article 6 elongate; gnathopod 2 with article 6 slightly expanded distally, palm transverse, defined by a single

spine; article 5 of pereopod 3 twice as wide as long, dactyl cultriform, broad, anterior margin distally serrate; article 2 of pereopod 5 subcircular.

Distribution: Natal, Madagascar.

Remarks: Rabindranath (1971) synonymized *Urothoe serrulidactylus* with *U. ruber* Giles but this is incorrect, as can be seen by comparing Rabindranath's figures with those of either K. H. Barnard (1955) or Ledoyer (1969). The dactyl of pereopod 3 in *serrulidactylus* is distinctly wide and cultriform and quite naked of setae, while that of *U. ruber* is very narrow, evenly tapering and bears a number of small setae. The palm of gnathopod 2 is also markedly chelate in *U. ruber* but more transverse in *serrulidactylus* and there are a number of differences in the minute structure of the mouth parts and antennae.

Urothoe tumorosa n. sp.

Fig. 6

Description of male (3.5 mm): Head as long as three pereon segments; eyes large, dark, separated dorsally by about $\frac{1}{3}$ of their diameter; antenna 1 (Fig 6A) with 6-articulate flagellum and 3-articulate accessory flagellum, peduncular articles subequal; antenna 2 (Fig 6K) as long as body, article 4 of peduncle heavily spinose, article 5 and flagellum bearing aesthataes, flagellum 36-articulate; mandible with very large circular molar, incisor simple, heavily chitinized, palp 3-articulate, articles 2 and 3 subequal, each twice article 1; palp of maxilla 1 bi-articulate, tipped with three long plumose setae, outer plate terminally bearing about ten strong serrate spines; maxilla 2 normal; maxilliped bearing 4-articulate palp, article 3 expanding distally from a very narrow base, outer lobe distally bearing five spine teeth interspersed with fine setae, inner plate terminating in two spines and five short setae.

Coxa 1 triangular, remaining coxae subquadrate, not produced (cf. *U. coxalis* n. sp.), but each bearing a few setae postero-distally; gnathopods similar, subchelate; article 5 of gnathopod 1 bearing nine strong spines on distal margin, palm undefined, minutely pectinate; article 5 of gnathopod 2 lacking spines, palm defined by two short spines, minutely pectinate; articles 5 and 6 of pereopods 1 and 2 posteriorly strongly spinose, dactyl bearing 3-4 pronounced knobs; pereopod 3 strongly spinose (Fig 6F), a group of very long plumose setae arising from inner margin of article 4, articles 5 and 6 about as wide as long, bearing rows of strong blunt spines and occasional plumose setae, dactyl wide, evenly tapering, bearing about seven pronounced knobs on anterior margin; pereopod 4 with posterior margin of article 4 bearing plumose setae, dactyl with anterior knobs; pereopod 5 like 4 but lacking plumose setae and considerably shorter.

Pleonal epimera 1-3 postero-distally rounded, the second bearing a prominent group of long plumose setae which extend to the posterior end of the body; peduncle of uropod 1 setose and bearing a lateral and two distal

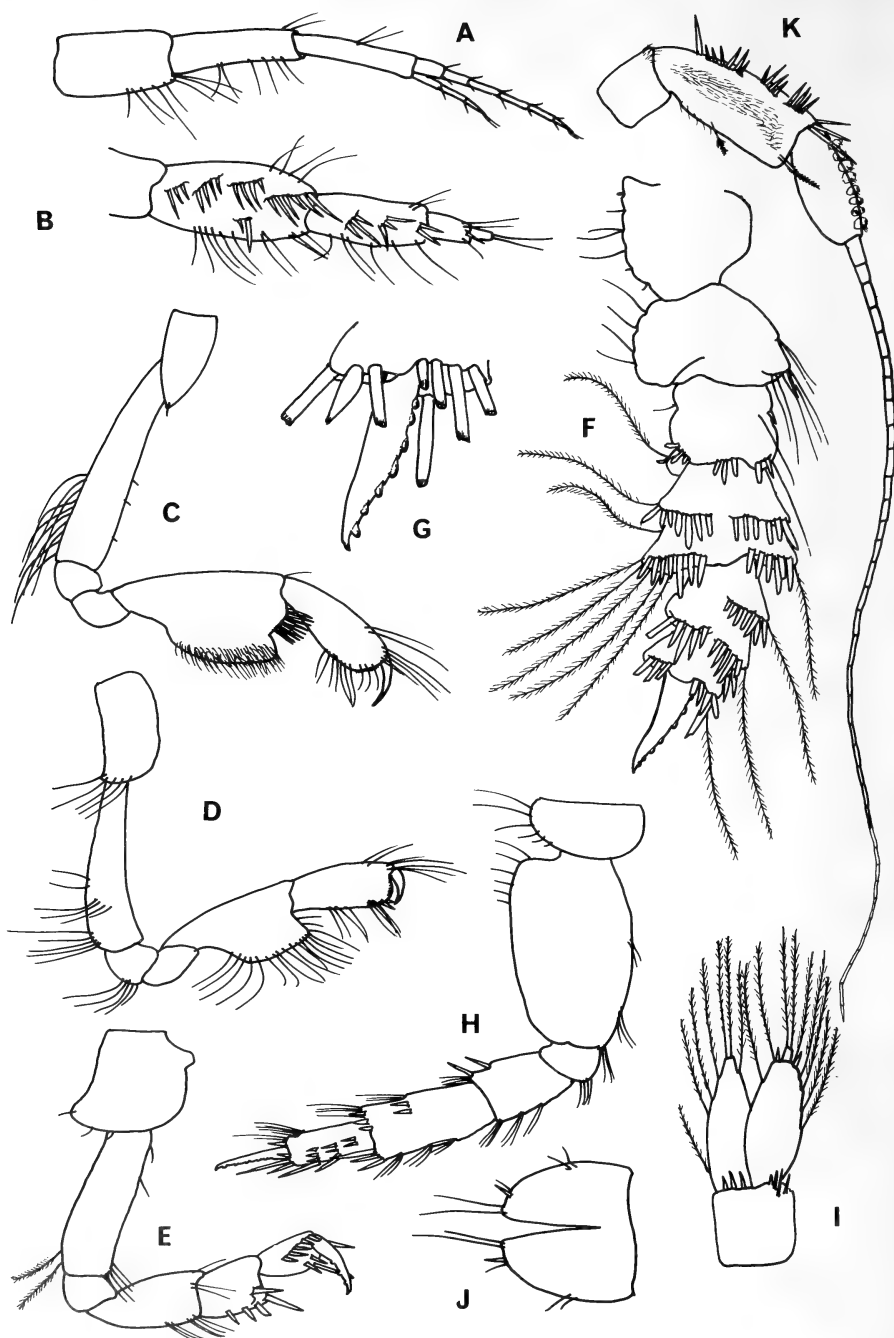


Fig. 6. *Urothoe tumorosa* n. sp.

Female, 3,5 mm: A—antenna 1; B—antenna 2; C—gnathopod 1; D—gnathopod 2; E—perceiopod 2; F—perceiopod 3; G—dactyl of perceiopod 3; H—perceiopod 5; I—uropod 3; J—telson.
Male 3,5 mm: K—antenna 2.

spines, outer ramus equal to peduncle and bearing a single mediodorsal spine, inner ramus naked, 80 per cent length of outer; uropod 2 half length of 1, peduncle with two strong distal spines, rami equal, unarmed; peduncle of uropod 3 quadrate, distally spinose, rami subequal, the outer with a minute second article, both rami marginally bearing plumose setae; telson (Fig. 6J) as long as broad, 80 per cent cleft, each lobe with a terminal spine and three setae and with two small lateral setae.

Holotype: SAM A13214, male, 3.5 mm.

Type-locality: NIWR/2/20A, 19 July 1972, 30°14'S/30°52'E, depth 44 m.

Female: Similar to the male except for the second antennae, which are much shorter than those of the male (Fig 6B), and the smaller third uropods (Fig 6I) which have fewer, shorter plumose setae than those of the male.

Relationships: The marked protuberances on the dactyls, particularly that of pereopod 3, are sufficient to identify this species. Stebbing (1906) quotes two other species, *U. marina* (Bate), and *U. irrostrata* Dana as possessing nodulose dactyls, but fuller descriptions of these species in Chevreux & Fage (1925) and Della Valle (1893) respectively show the dactyls to be minutely serrulate in both cases.

Material: NIWR/UM/M2B(1), NIWR/2/20A(2), NIWR/2/33D(1).

Family **Isaeidae**

Cheiriphotis megacheles (Giles, 1885)

Cheiriphotis durbanensis K. H. Barnard, 1916: 247.

Cheiriphotis megacheles: J. L. Barnard, 1962a: 17, fig. 4.

Records: Durban Bay (K. H. Barnard 1916 as *C. durbanensis*); Durban (Stebbing 1918).

Distribution: Indo-Pacific.

Chevalia aviculae Walker, 1904

Chevalia aviculae: J. L. Barnard, 1971: 88, fig. 42.

Records: NAD 16N(7); NIWR/UM/D3B(1), NIWR/UM/P1B(1), NIWR/2/36H(4).

Distribution: Circumtropical and warm temperate.

Gammaropsis afra (Stebbing, 1888)

Gammaropsis afra: J. L. Barnard, 1970b: 170, fig. 108.

Records: 29/31/430 m (J. L. Barnard 1961).

Distribution: Almost circumtropical.

Gammaropsis atlantica (Stebbing, 1888) **new synonymy**

Eurystheus imminens K. H. Barnard, 1916: 250; 1937: 165, fig. 11.

Gammaropsis atlantica: J. L. Barnard, 1970b: 174, figs 111–113.

Records: NIWR/1/26F(1), NIWR/UM/D3A(1), NIWR/UM/R3B(1), NIWR/2/24E(3), NIWR/2/30M(5), NIWR/2/36B(13); ABD 8Q(2); NAD 4S(2) NAD 11R(11), NAD 19G(10), NAD 56A(41), NAD 61A(1), NAD 64F(6), NAD 66R(3), NAD 70V(2), NAD 81H(1), NAD 90T(22), NAD 92N(7), NAD 92 (P); 'Morewood cove' 50 m (K. H. Barnard 1916 as *E. imminens*).

Distribution: Almost circumtropical.

Remarks: K. H. Barnard (1916) erected *G. imminens* on the basis of two characters—the relative sizes of the palmar teeth of gnathopod 2 male, and the shape of the eyes ('elongate oval'). I have examined his type material and find the eyes to be of a shape consistent with those of *G. atlantica* from the same area (vertically elongate but not markedly constricted dorsally). Although the relative size of the palmar teeth is unusual their general shape is consistent with *G. atlantica*, and this cannot be regarded as taxonomically significant in the light of the variability of *G. atlantica* which has been demonstrated in recent years (e.g. J. L. Barnard 1970b). Moreover, the fact that the specimens were found amongst samples of *G. atlantica* suggests that they merely represent aberrations of the normal form.

Gammaropsis chelifera (Chevreux, 1901)

Eurystheus semichelatus K. H. Barnard, 1957: 8, fig. 5.

Gammaropsis chelifera: Ledoyer, 1972: 239, pl. 54A.

Gammaropsis semichelatus: Griffiths, 1972: 290.

Records: NA 191J(8).

Distribution: Indian Ocean.

Gammaropsis holmesi (Stebbing, 1908) **new synonymy**

Eurystheus holmesi Stebbing, 1908: 85, pl. 14A. K. H. Barnard, 1955: 95, figs 48 A–D.

Eurystheus semidentatus K. H. Barnard, 1916: 250, pl. 28, figs 13, 14.

Records: NAD 7D(2), NAD 19Q(14); Durban (Stebbing 1918).

Diagnosis: Gnathopod 2 powerful, hind margin much shorter than oblique, dentate palm, palm defined by a small tooth; hind margins of article 2 of pereopods 3–5 strongly serrate posteriorly; pleon segment 4 dorsally tridentate, median tooth the smallest, segment 5 with a pair of dorso-lateral teeth.

Distribution: Endemic, Natal to Saldanha Bay.

Remarks: As originally described by K. H. Barnard (1916), *G. semidentatus* could be distinguished from *G. holmesi* by the less marked and more regular serrations along the posterior margin of article 2 of pereopods 3–5, and by differences in the teeth of the palm of gnathopod 2. However it has since been

found that Stebbing's original material was unusually well developed as regards these features, the usual form of *G. holmesi* being described and figured by K. H. Barnard (1955). As can be seen by comparing these figures with those depicting *semidentatus*, the two species have become indistinguishable, *holmesi* merely representing a more highly developed phenotype of *semidentatus*. Since *holmesi* has preference, *semidentatus* thus falls into synonymy with it.

Photis longimanus Walker, 1904

Photis longimanus: K. H. Barnard, 1916: 244. Sivaprakasam, 1970: 567, fig. 8.

Records: Durban Bay (K. H. Barnard 1916).

Distribution: Indian Ocean, extending to South West Africa.

Photis kapapa J. L. Barnard, 1970

Photis kapapa J. L. Barnard, 1970b: 192, figs 124, 125.

Records: NIWR/UM/R3C(5), NIWR/2/27H(3), NIWR/2/33F(3); NAD 19E(23), NAD 56D(2), NAD 64G(1).

Distribution: Hawaii, east coast of southern Africa.

Photis uncinata K. H. Barnard, 1932

Photis longicaudata: K. H. Barnard, 1916: 243, pl. 28, fig. 26.

Photis uncinata K. H. Barnard, 1932: 223, fig. 138.

Records: NIWR/1/6B(1), NIWR/1/14D(2), NIWR/UM/D3C(1), NIWR/2/22B(1); 29/31/50 m, 'Morewood Cove' 50 m (K. H. Barnard 1916).

Diagnosis: Articles 5 and 6 of gnathopod 1 subequal, palm very oblique, faintly denticulate; article 2 of gnathopods 1 and 2 antero-distally terminating in a small curved acute process tipped by two setae; article 6 of gnathopod 2 oblong, defining angle rectangular, slightly produced, palm nodulose, dactyl serrate; outer ramus of uropod 3 very small.

Distribution: Endemic to South Africa.

Family **Ischyroceridae**

Ischyrocerus anguipes Kröyer, 1838

Ischyrocerus anguipes: Schellenberg, 1953: 120, fig. 7A-C.

Records: NIWR/3/30S(1), NIWR/2/35C(1).

Distribution: Atlantic, Indo-Pacific.

Jassa falcata (Montagu, 1808)

Jassa falcata: Sexton & Reid, 1951: 30-47, pls 4-30. J. L. Barnard, 1969a: 155, figs 38, 39.

Records: DBN 131P(1); D 276(2); NA 244F(23).

Distribution: Cosmopolitan.

Family **Leucothoidae***Leucothoe ctenochir* K. H. Barnard, 1925

Leucothoe ctenochir K. H. Barnard, 1925: 342, pl. 34, fig. 8.

Records: NAD 4P(7); Port Shepstone (K. H. Barnard 1925).

Diagnosis: Readily identified by the form of the palm of gnathopod 2 which is cut into five or six regular comb-like teeth, the tooth nearest the finger-hinge obscurely bifid; third pleonal epimeron postero-distally subquadrate, lacking a posterior sinus; antenna 1 extending to pereon segment 3.

Distribution: Endemic to east coast of South Africa.

Leucothoe dolichoceras K. H. Barnard, 1916

Leucothoe dolichoceras K. H. Barnard, 1916: 157, pl. 26, fig. 14; 1925: 343.

Records: NIWR/2/36Q(1); NAD 4Q(1).

Diagnosis: Antenna 1 extending to pleon segment 3 (unusually long); article 6 of gnathopod 1 long and narrow, palm with two large blunt-tipped tubercles near finger-hinge, a third proximal to them and a series of small denticles near defining angle; dactyl equal to palm, a deep semicircular incision bounded by a denticle near its base (this form of gnathopod 2 only fully developed in specimens over 8 mm); third pleonal epimeron acutely produced with a deep sinus above postero-distal corner.

Distribution: Endemic to South Africa.

Leucothoe richiardi Lessona, 1865

Leucothoe richiardi: Sivaprakasam, 1967: 385, fig. 2.

Records: NAD 4R(6).

Diagnosis: Antenna 1 extending to pereon segment 3; article 6 of gnathopod 2 elongate oval, palm convex, denticulate distally; third pleonal epimeron postero-distally acute, a sinus above corner (obscure in females).

Distribution: Mediterranean, India, South Africa.

Leucothoe spinicarpa (Abildgaard, 1789)

Leucothoe spinicarpa: K. H. Barnard, 1916: 148. Sivaprakasam 1967: 384, fig. 1.

Records: NIWR/3/24F(4); NAD 90U(22); NA 243B(1); 30/30/50 m (K. H. Barnard 1916).

Distribution: Cosmopolitan.

Family **Liljeborgiidae***Liljeborgia epistomata* K. H. Barnard, 1932

Liljeborgia epistomata K. H. Barnard, 1932: 144, fig. 83; 1955: 89, fig. 44.

Records: NAD 15M(2).

Diagnosis: The male differs considerably from the female and is relatively rare. Male coxa 1 ovoid, enormously enlarged; article 6 of gnathopod 2 $1\frac{1}{2}$ times as long as broad, palm oblique, sinuous, a prominent bilobed tooth near finger-hinge, dactyl with 7-8 large serrations, closing into a shallow pit on inner surface of hand which is armed by three spines. Female coxa 1 normal, gnathopod 2 palm not toothed. Both sexes lack eyes and dorsal teeth on pleon segment 1; pleon segments 2, 4 and 5 have single medio-dorsal teeth, those of segments 4 and 5 forming the termination of medio-dorsal keels.

Distribution: Endemic, Saldanha Bay to Natal.

Family **Lysianassidae***Amaryllis macrophthalma* Haswell, 1880

Amaryllis macrophthalma: J. L. Barnard, 1972: 262, figs 156-158.

Records: NIWR/1/26C(1), NIWR/1/27D(1), NIWR/UM/M3C(2), NIWR/2/17B(2), NIWR/2/32B(8), NIWR/2/36C(13); NA 205J(1); 30/30/50 m, 29/31/100 m (K. H. Barnard 1916).

Distribution: Southern Hemisphere.

Hippomedon longimanus (Stebbing, 1888)

Hippomedon longimanus Stebbing, 1888: 643, pl. 12. K. H. Barnard, 1916: 125.

Records: 29/31/80 m (K. H. Barnard 1916).

Diagnosis: Eyes absent; article 1 of antenna 1 longer than articles 2 plus 3, article 1 of flagellum elongate; gnathopods 1 and 2 long and slender, article 5 longer than 6; pleon segment 4 dorsally depressed anteriorly and posteriorly carinate; third pleonal epimeron with a short point postero-inferiorly; telson 60 per cent cleft, apices somewhat divergent, each ending in a spine.

Distribution: Atlantic, extending to Natal.

Hippomedon onconotus (Stebbing, 1908)

Tryphosa onconotus Stebbing, 1908: 65, pl. 35.

Records: NIWR/UM/M1B(1).

Diagnosis: Eyes absent; article 1 of antenna 1 as long as 2 plus 3; article 5 of gnathopods 1 and 2 longer than article 6; pleon segment 4 with a deep dorsal depression followed by an upturned acute triangular process; third pleonal

epimeron smoothly rounded; telson 80 per cent cleft, each lobe with an apical and a lateral spine and two proximal setae.

Distribution: Endemic to South Africa.

Lysianassa ceratina (Walker, 1889)

Lysianassa cubensis: K. H. Barnard, 1916: 120.

Lysianassa ceratina: Chevreux & Fage, 1925: 42, fig. 23.

Records: NIWR/1/27J(2), NIWR/2/27C(4), NIWR/2/30A(6); NA 244H(3), G 15N; M 19E.

Distribution: Mediterranean, Atlantic, Indian Ocean.

Lysianassa variagata (Stimpson, 1855)

Lysianassa variagata: Stebbing, 1888: 682. pl. 23.

Records: NAD 4M(2), NAD 81K(3).

Distribution: Africa south of the equator.

Microlysias xenoceras Stebbing, 1918

Microlysias xenoceras Stebbing, 1918: 64, pl. 9.

Records: Durban (Stebbing 1918).

Distribution: Endemic, Durban to Plettenberg Bay.

Trischizostoma remipes Stebbing, 1908

Trischizostoma remipes Stebbing, 1908: 61, pl. 34. K. H. Barnard, 1925: 321.

Records: NAD 11S(1).

Diagnosis: Article 6 of gnathopod 1 very large, showing some torsion, palm elongate, evenly convex, minutely serrulate, dactyl curved, inner margin smooth; eyes very large, nearly meeting on top of head; rostrum small; accessory flagellum of antenna 1 of a single laminar joint followed by a short linear one; article 6 of pereopod 5 slightly longer and wider than 5, forming a narrow blade-like lamina; telson 40 per cent cleft.

Distribution: Endemic, Natal to False Bay.

Trischizostoma serratum K. H. Barnard, 1925

Trischizostoma serratum K. H. Barnard, 1925: 320, pl. 34, fig. 1.

Records: 'Various localities on Natal coast' (K. H. Barnard 1925).

Diagnosis: Close to *T. remipes* but differing in the form of gnathopod 1 which has a straight or concave palm with defining angle produced into a blunt point with 1 or 2 stout blunt spines, palm entire, armed with seven stout marginal

and five submarginal spines, inner margin of dactyl with a series of conical denticles at regular intervals.

Distribution: Endemic, Natal to False Bay

Tryphosella normalis K. H. Barnard, 1955

Tryphosella normalis K. H. Barnard, 1955: 80, fig. 39.

Records: NIWR/1/26E(2), NIWR/1/27H(6), NIWR/UM/P1D(1), NIWR/2/30D(2).

Distribution: Endemic, Natal to South West Africa.

Uristes natalensis K. H. Barnard, 1916

Uristes natalensis K. H. Barnard, 1916: 126.

Records: Port Shepstone (K. H. Barnard 1916).

Diagnosis: Coxa 1 widening distally, oblong, not greatly reduced; pleon segment 4 somewhat depressed basally but neither carinate nor produced; telson oblong, apices divergent.

Distribution: Endemic to east coast of South Africa.

Family **Ochlesidae**

Ochlesis lenticulosus K. H. Barnard, 1940

Ochlesis lenticulosus K. H. Barnard, 1940: 447, fig. 23.

Records: NIWR/2/30T(1).

Diagnosis: Pereon and pleon dorsally carinate, the carinae of pereon segment 7 and pleon segments 1 and 2 produced posteriorly into a blunt dorsal projection, pleon segment 3 with an upstanding triangular projection about the middle of its length; third pleonal epimeron postero-distally produced into a sharply upturned tooth; lower distal margins of articles 1 and 2 of antenna 1 produced into spinose projections.

Distribution: Endemic, Natal to False Bay.

Family **Phliantidae**

Palinnotus natalensis K. H. Barnard, 1940

Palinnotus natalensis K. H. Barnard, 1940: 445, fig. 22.

Records: D 279; Isipingo (K. H. Barnard 1940); Port Shepstone (K. H. Barnard 1955).

Diagnosis: Body dorsally depressed, coxae splayed; article 2 of pereopod 5 strongly expanded, as wide as long in adults; article 4 distally strongly lobed; uropod 3 lacking rami.

Distribution: Natal, India.

Family **Phoxocephalidae***Mandibulophoxus stimpsoni* (Stebbing, 1908)

Pontharpinia stimpsoni Stebbing, 1908: 75, pl. 11.

Mandibulophoxus stimpsoni: J. L. Barnard, 1957: 436-438, figs 3, 4.

Records: NIWR/1/5A(2), NIWR/1/14F(1), NIWR/1/24A(1), NIWR/1/26A(8), NIWR/1/27A(5), NIWR/UM/R3E(1), NIWR/UM/P5B(1), NIWR/UM/M1A(2), NIWR/UM/M2A(3), NIWR/UM/M3A(3), NIWR/2/17A(3), NIWR/2/19A(1), NIWR/2/21F(1), NIWR/2/22A(1), NIWR/2/23A(2), NIWR/2/27B(5), NIWR/2/29A(1), NIWR/2/30B(5), NIWR/2/32A(1), NIWR/2/33A(4), NIWR/2/35A(2), NIWR/2/36A(1); NAD 27C(1).

Diagnosis: Eyes present; rostrum extending beyond tip of peduncle of antenna 1, apex drawn out into a curved downturned point; third pleonal epimeron with an oblique setal row on its exterior surface; rami of uropods 1 and 2 dorsally and apically spinose; telson cleft to base.

Distribution: West and southern Africa.

Family **Podoceridae***Laetmatophilus durbanensis* K. H. Barnard, 1916

Laetmatophilus durbanensis K. H. Barnard, 1916: 275.

Records: Durban Bay (K. H. Barnard 1916).

Diagnosis: Pereon transversely ridged; gnathopod 1 with article 6 not at all widened, narrower than article 5, palm smooth, not defined from hind margin; article 2 of gnathopod 2 male with two anterior keels, both apically acute, article 6 broadly ovate, palm straight, with a low denticulate process extending from the finger-hinge about $\frac{1}{3}$ way along the palm and a pointed tooth proximal to it, dactyl nearly straight, matching palm.

Distribution: The above record is the only one to date.

Laetmatophilus purus Stebbing, 1888

Laetmatophilus purus Stebbing, 1888: 1198, pl. 132.

Records: NIWR/2/30E(18).

Distribution: Endemic, South West Africa to Moçambique.

Laetmatophilus tridens K. H. Barnard, 1916

Laetmatophilus tridens K. H. Barnard, 1916: 275, pl. 28, fig. 22.

Records: NAD 15L(1).

Distribution: Endemic, Moçambique to Saldanha Bay.

Podocerus africanus K. H. Barnard, 1916

Podocerus africanus K. H. Barnard, 1916: 278, pl. 28, figs 24-25; 1937: 176, fig. 19.

Records: NA 244D(30); Port Shepstone (K. H. Barnard 1925).

Distribution: Arabia, Natal to South West Africa.

Podocerus brasiliensis (Dana, 1853)

Podocerus brasiliensis: J. L. Barnard, 1970: 237, figs 156-157.

Records: DBN 2W(15), DBN 62J(C), DBN 131J(A), DBN 131K(1), DBN 251C(C), DBN 271F(2), DBN 379D(P); Durban Bay (K. H. Barnard 1916 as *P. synapochir*).

Diagnosis: Body lacking dorsal processes; coxa 1 weakly produced forwards, apically rounded; male gnathopod 2 with article 2 not anteriorly keeled, obscurely lobed distally, palm occupying whole posterior margin of article 6, undefined and smooth except for a slight distal bulge, dactyl half length of palm; peduncles and inner rami of uropods 1 and 2 moderately and irregularly spinose.

Distribution: Cosmopolitan in tropical and temperate seas.

Podocerus inconspicuus (Stebbing, 1888)

Podocerus palinuri K. H. Barnard, 1916: 277, pl. 28, fig. 23.

Podocerus inconspicuus: Nagata, 1965: 322, fig. 43.

Records: NIWR/2/19A(1); NA 191H(1); Durban (Stebbing 1918).

Distribution: Indo-Pacific, extending along west coast of South Africa.

Podocerus multispinis K. H. Barnard, 1925

Podocerus multispinis K. H. Barnard, 1925: 367, pl. 34, fig. 18.

Records: NAD 4V(2).

Diagnosis: Body not dorsally keeled but bearing two transverse rows of 3 spiniform tubercles on segment 1 and a single row on each of segment 2-7; coxa 1 produced forwards to level of the eye, apically acute; male gnathopod 2 with article 2 strongly keeled on inner and outer anterior margins, both keels ending in rounded setiferous lobes; palm 60% length of article 6, defined by a strong conical tooth, an obscure bifid tooth halfway along the palm and another square topped tooth near the finger-hinge, dactyl almost as long as palm; inner margins of peduncles and inner ramis of uropods 1 and 2 with comb-like rows of closely set spines.

Distribution: Endemic, Natal to Saldanha Bay.

Family **Stenothoidae***Proboloides rotunda* (Stebbing, 1917)

Metopa rotundus Stebbing, 1917: 39, pl. 7A.

Proboloides rotunda: K. H. Barnard, 1940: 444.

Records: NIWR/2/30P(1), NIWR/2/36N(11); NAD 19M(1).

Diagnosis: Body round; flagellum of antenna 1 and 2 shorter than peduncle, accessory flagellum absent; article 6 of gnathopod 1 parallel-sided, twice as long as broad, palm smooth, oblique; gnathopod 2 much larger than 1, palm oblique, convex, serrate near finger-hinge then abruptly stepped to form a cavity within which the dactyl closes; article 4 of pereopods 4 and 5 produced posteriorly into an acute lobe extending to the end of article 5; peduncle of uropod 3 longer than ramus, article 1 of ramus longer than spiniform second article.

Distribution: Endemic to South Africa.

Stenothoe gallensis Walker, 1904

Stenothoe gallensis: K. H. Barnard, 1925: 344. J. L. Barnard, 1955: 3, fig. 1; 1971: 120, figs 62–63.

Records: NAD 17Q(1); Durban (K. H. Barnard 1916); Port Shepstone (K. H. Barnard 1925).

Distribution: Cosmopolitan.

Remarks: K. H. Barnard's (1925) identification was queried by J. L. Barnard (1955) on the basis of the shape of uropod 3. I have examined the single male K. H. Barnard (1925) referred to, but find the third uropods to be missing. However, other material from South Africa conforms with his description, the third uropod differing from the usual form (figured in J. L. Barnard 1971) in that article 2 of the ramus is proximally almost circular and has an almost straight distal process arising from the superior half of its distal margin, the process is ridged in the usual pattern for the species. The process is *not* demarcated in any way from the proximal part of the article. Although the shape of the third uropod is unusual, I feel that in the light of increasing variability which has been found in this species, and its relative *S. valida* Dana, in recent years, it would be unwise to erect a new species for this form.

Stenothoe valida Dana, 1853

Stenothoe valida: Sivaprakasam, 1967: 373, fig. 2 a–b. J. L. Barnard, 1970b: 250, fig. 165.

Records: DBN 2U(C), DBN 62H(C), DBN 131M(P), DBN 251G(1), DBN 379C(P), DBN 396E(P); Durban (K. H. Barnard 1925).

Distribution: Cosmopolitan in tropical and temperate seas.

Family **Synopiidae***Tiron australis* Stebbing, 1908

Tiron australis Stebbing, 1908: 79, pl. 38.

Records: NIWR/2/20C(1), NIWR/2/36S(2).

Diagnosis: Accessory eye of four ommatidea; mandible with 3-articulate palp; inner plate of maxilla 2 with a medial submarginal row of setae; dactyls of pereopods stubby but apically sharp; article 2 of pereopods 4 and 5 not strongly setose, that of 5 crenulate posteriorly; pleonites 1-3 dorsally crenulate; each lobe of telson with a median row of large spines.

Distribution: Endemic to east and south coasts of South Africa.

Superfamily TALITROIDEA

Family **Hyaellidae***Afrochiltonia capensis* (K. H. Barnard, 1916)

Chiltonia capensis K. H. Barnard, 1916: 224, pl. 27, figs 38-40.

Afrochiltonia capensis: K. H. Barnard, 1955: 93.

Records: STL 89G(A), STL 102C(C); KOS 62B(3), KOS 74G(5), KOS 78H(6), KOS 81E(1), KOS 82F(1); RHB 129Q(2); UMK 19W(C), UMK 23W(2), UMK 25C(P), UMK 26H(C), UMK 27N(C), UMK 29A(A); EDW 3B(C).

Diagnosis: Since the genus is monotypic the generic characters diagnose the species. Habitat estuarine and brack water; maxilla 1 lacking palp; gnathopods of both sexes subchelate; male gnathopod 2 not larger than gnathopod 1; female gnathopod 2 like gnathopod 1; male pleopod 1 normal; uropod 3 lacking rami; telson entire.

Distribution: Endemic, Zululand to Saldanha Bay.

Parhyalella natalensis (Stebbing, 1917)

Exhyalella natalensis: Stebbing, 1918: 67, pl. 11.

Parhyalella natalensis: K. H. Barnard, 1925: 359.

Records: Durban (Stebbing 1918; K. H. Barnard 1925).

Diagnosis: Flagellum of antenna 1 and 2 at least as long as peduncle; article 5 of gnathopod 1 male larger than 6; article 5 of gnathopod 2 male with a narrow posterior lobe intervening between articles 4 and 6, palm oblique, elongate, spine fringed, having a very short hind margin; uropod 3 very small, peduncle much larger than ramus; telson entire.

Distribution: Not recorded outside Durban.

Family **Hyalidae***Hyale grandicornis* (Kröyer, 1845)

Hyale grandicornis: Stephensen, 1949: 33, figs 14, 15.

Records: G 15F; V 28L; D 118; M 19H; NA 243C(1), NA 244G(18); Port Shepstone, Isipingo, Port Edward (K. H. Barnard 1955).

Distribution: Cosmopolitan in tropical and temperate seas.

Family **Talitridae***Orchestia ancheidos* (K. H. Barnard, 1916)

Talorchestia ancheidos K. H. Barnard, 1916: 221, pl. 27, figs 35, 36.

Orchestia ancheidos: Ruffo, 1958: 43, figs 3, 4.

Records: STL 11D(4), STL 18D, STL 52G, STL 67B, STL 73A, STL 77A, STL 135B(2), STL 148B(8), STL 171A(2), STL 232D, STL 270B, STL 299R(2), STL 317D(2), STL 342G(A), STL 343J(5), STL 344; KOS 6A(A), KOS 15A(2), KOS 78G(3); RHB 38A(15), RHB 93A(3), RHB 132D(20); UMK 24N; SHP 5B(C); Umlalazi estuary (Hill 1966).

Distribution: Madagascar, Moçambique, South Africa.

Orchestia rectipalma (K. H. Barnard, 1940)

Parorchestia rectipalma K. H. Barnard, 1940: 473, fig. 32.

Records: STL 89F(A), STL 102D(1); RHB 124N(1), RHB 129C(3); EDW 3A(C); UMK 19F, UMK 29C(P), UMK 33C(8).

Distribution: Endemic; Natal to South West Africa.

Suborder CAPRELLIDEA

Family **Aeginellidae***Metaprotella macrodactylos* Stebbing, 1910

Metaprotella macrodactylos Stebbing, 1910: 469, pl. 48A.

Records: NIWR/2/30K(1).

Diagnosis: Last two thoracic segments distinct but not movable upon each other; head bearing an acute forward-directed process, rest of the body lacking dorsal processes; pereopods 1 and 2 minute, less than $\frac{1}{4}$ length of branchiae; second gnathopods large, hand very long and bearing a pronounced acute tooth on the palm near the articulation of the dactyl, dactyl extending whole length of hand.

Distribution: Endemic, this is only the second record of this species, the first being from the Port Elizabeth area.

Monoliropus falcimanus Mayer, 1904

Monoliropus falcimanus: Sivaprakasam, 1967: 382, fig. 4G-H.

Records: ABD 14K(1).

Distribution: Indian Ocean.

Pseudaeginella tristanensis (Stebbing, 1888)

Pseudaeginella tristanensis: Stephensen, 1949: 52, fig. 23.

Records: NIWR/2/30U(1); NA 244B(1).

Diagnosis: Branchiae on pereon segments 2 and 3; pereopods 1 and 2 absent, pereopod 3 6-articulate; abdomen lacking appendages; pereon segment 1 with a large upright antero-dorsal tooth and a smaller posterior one, segments 2-4 each with three dorsal tubercles, the largest in the centre of the segments, the others sometimes obscure; gnathopod 2 with a small acute tooth half way along the palm and two smaller rounded teeth distally.

Distribution: Tristan da Cunha, South Africa.

Family **Caprellidae***Caprella cicur* Mayer, 1903

Caprella cicur Mayer, 1903: 75, 97, pl. 4, figs 5-7, pl. 8, figs 3-5.

Records: G 15K; U 28H; J 11C.

Diagnosis: Head with short rostral point; basis of gnathopod 2 shorter than pereon segment 2, outer margin anteriorly keeled, the keel ending in an acute point; a spine ventrally between the insertions of gnathopod 2, hand of male gnathopod 2 elongate, palm defined by an acute forward directed process, a triangular tooth near finger-hinge.

Distribution: Endemic, Natal to west coast of South Africa.

Caprella danilevski Czerniavski, 1868

Caprella danilevskii: Chevreux & Fage, 1925: 454, fig. 432. McCain, 1968: 22-25, figs 10-11.

Records: J 11C.

Distribution: Widespread in tropical seas.

Caprella equilibra Say, 1818

Caprella equilibra: McCain, 1968: 25-30, figs 12-13.

Records: DBN 2X(A), DBN 131C(P), DBN 241 W(1), DBN 251A(A), DBN 379A(C), DBN 396F(C); NAD 15J(6); Durban (K. H. Barnard 1916).

Distribution: Cosmopolitan, 0-300 m.

Caprella laevipes Mayer, 1903

Caprella laevipes Mayer, 1903: 108, pl. 5, fig. 2, pl. 8, figs 14-16.

Records: 'Port Natal' (= Durban, Mayer 1903).

Diagnosis: Head with large anteriorly directed rostral spine; basis of gnathopod 2 longer than pereon segment 2; no spine between insertions of second gnathopods, hand elongate and expanding distally in adult males, palm with two strong teeth and a distal rectangular projection; pereopods 5-7 lacking grasping spines (distinguishing the species from *C. scaura*).

Distribution: Endemic, Natal to west coast of South Africa.

Caprella natalensis Mayer, 1903.

Caprella acutifrons var. *natalensis*: Mayer, 1903: 81, pl. 3, figs 22, 23.

Caprella penantis (non Leach, 1814): Stebbing, 1910: 465.

Caprella penantis var. *natalensis*: K. H. Barnard, 1916: 281.

Caprella angusta: Laubitz, 1970: 40, fig. 11.

Caprella natalensis: Laubitz, 1972: 47, pl. 9, figs F,G, pl. 10, figs F-K.

Records: Durban (Mayer 1903; K. H. Barnard 1916).

Diagnosis: Head with anteriorly directed rostrum; basis of gnathopod 2 shorter than pereon segment 2; no spine between insertions of second gnathopods, hand twice as long as broad, palm sparsely setose with proximal poison tooth and distal rectangular projection.

Distribution: Pacific North America, Tristan de Cunha, South Africa.

Remarks: This form was originally described by Mayer as one of twenty varieties of *C. acutifrons* which he recognized. These varieties were analysed by McCain (1968) who assigned eight of them including var. *natalensis*, to *C. penantis*. Laubitz (1970) subsequently elevated one of these eight, *C. angusta*, to specific level but then (1972) synonymized this with a newly elevated *C. natalensis*. This species can be distinguished from *C. penantis* by its long pereonite 5 (as long as 6+7) and the sparse setification of the palm of gnathopod 2, as well as the absence of pleura, which are usually well developed in adult *C. penantis*.

Caprella penantis Leach, 1814

Caprella penantis: McCain, 1968: 33-40, figs 15-16.

Records: D 272; NA 244A (26).

Distribution: Cosmopolitan in tropical and temperate seas.

Caprella scaura Templeton, 1836

Caprella scaura: McCain, 1968: 40-44, figs 17-18.

Records: DBN 131E(1).

Distribution: Cosmopolitan.

Paracaprella pusilla Mayer, 1890

Paracaprella pusilla: McCain, 1968: 82-86, figs. 32 a-b, 41, 42, 53.

Records: DBN 131D(1).

Diagnosis: Mandibular palp absent; antero-ventral margin of male pereon segment 2 acutely produced forwards; basis of gnathopod 2 short, a distinct hump on posterior margin near origin, palm with proximal grasping spine followed by a tooth, a pronounced excavation midway along palm; pereopods 1 and 2 2-articulate; pereopod 3 6-articulate.

Distribution: Cosmopolitan in tropical and temperate seas.

Family **Cyamidae***Cymus balaenopterae* K. H. Barnard, 1931

Cymus balaenopterae: K. H. Barnard, 1932: 309, fig. 171.

Records: Ectoparasitic on a fin whale, Durban (K. H. Barnard 1932).

Diagnosis: Maxilliped with palp; body narrow in dorsal view, parallel sided in male, ovate in female; pereon segment 1 completely fused with head, pereon segment 2 not laterally hooked; branchiae on segments 3 and 4 single, about as long as segments 2 and 3, male branchiae with single short pointed accessory gills; male with a pair of ventral tubercles on each of pereon segments 6 and 7; female with a pair of oblong ventral processes on segment 5, and a pair of tubercles on each of segments 6 and 7.

Distribution: Widespread on fin whales and blue whales.

Cymus boopis Lutken, 1873

Paracyamus boopis: K. H. Barnard, 1932: 312.

Cymus boopis: Margolis, 1955: 124, figs 7-12.

Records: Ectoparasitic on humpback and sperm whales, Durban (K. H. Barnard 1932).

Diagnosis: Maxillipedal palps absent, body ovate (but more slender than *C. erraticus*) pereon segment 2 not postero-laterally hooked; branchiae single with the bifurcate accessory gills in male shorter than pereon segments 2-5; male with one pair of ventral spines on each pereon segments 5-7, female with 2 pairs on segment 5 and one pair each on 6 and 7.

Distribution: Widespread on humpback whales.

Cymus erraticus Roussel de Vauzème, 1834

Paracyamus erraticus: K. H. Barnard, 1932: 310, fig. 172.

Cymus erraticus: Margolis, 1955: 132, figs 1-6.

Records: Humpback whale, Durban (Stebbing 1910).

Diagnosis: Maxilliped with or without palps; body broadly ovate, pereon segment 2 postero-laterally produced into a forwardly directed hooked process; branchiae single, as long as pereon segments 2-7 and with small bifid accessory lobe in adult male; male with 2 pairs of ventral spines on segments 5 and 6 and a single pair on 7, female with a single pair of spines on segments 5 and 7 and two pairs on 6.

Distribution: Widespread on right whales.

Family **Phtisicidae**

Phtisica marina Slabber, 1769

Phtisica marina: K. H. Barnard, 1916: 283. McCain, 1968: 91-97, fig. 46.

Records: 30/30/80 m (K. H. Barnard 1916).

Distribution: Principally Atlantic but extending to Moçambique, Mediterranean and Black Sea.

Caprellina longicollis (Nicolet, 1849)

Caprella longicollis: McCain, 1969: 289, fig. 2.

Records: DBN 404A(C).

Distribution: Southern oceans, Mediterranean.

Subfamily **Phtisicinae**

Chaka n. gen.

Diagnosis: Flagellum of antenna 2 tri-articulate, swimming setae present; mandible with 3-articulate palp, setal formula of terminal article 1-X-1, molar absent; outer lobe of maxilliped equal to inner lobe; gills on pereonites 2-4; pereopods 1 and 2 fully developed, pereopod 3 tri-articulate; abdomen of male and female with two pairs of bi-articulate appendages.

Type-species: *Chaka leoni* n. sp.

Relationships: The configuration of the pereopods in this genus is unique. Other genera in the subfamily *Phtisicinae* have five or six-articulate third pereopods, while genera in the subfamily *Dodecadinae* have pereopods 1 and 2 more or less reduced.

Chaka leoni n. sp.

Figs 7, 8

Description of male (11 mm): Head produced into a short flat-lying process (Fig. 7A), antenna 1 about as long as first five pereon segments, flagellum less than half peduncle, 11-articulate; antenna 2 shorter than peduncle of antenna

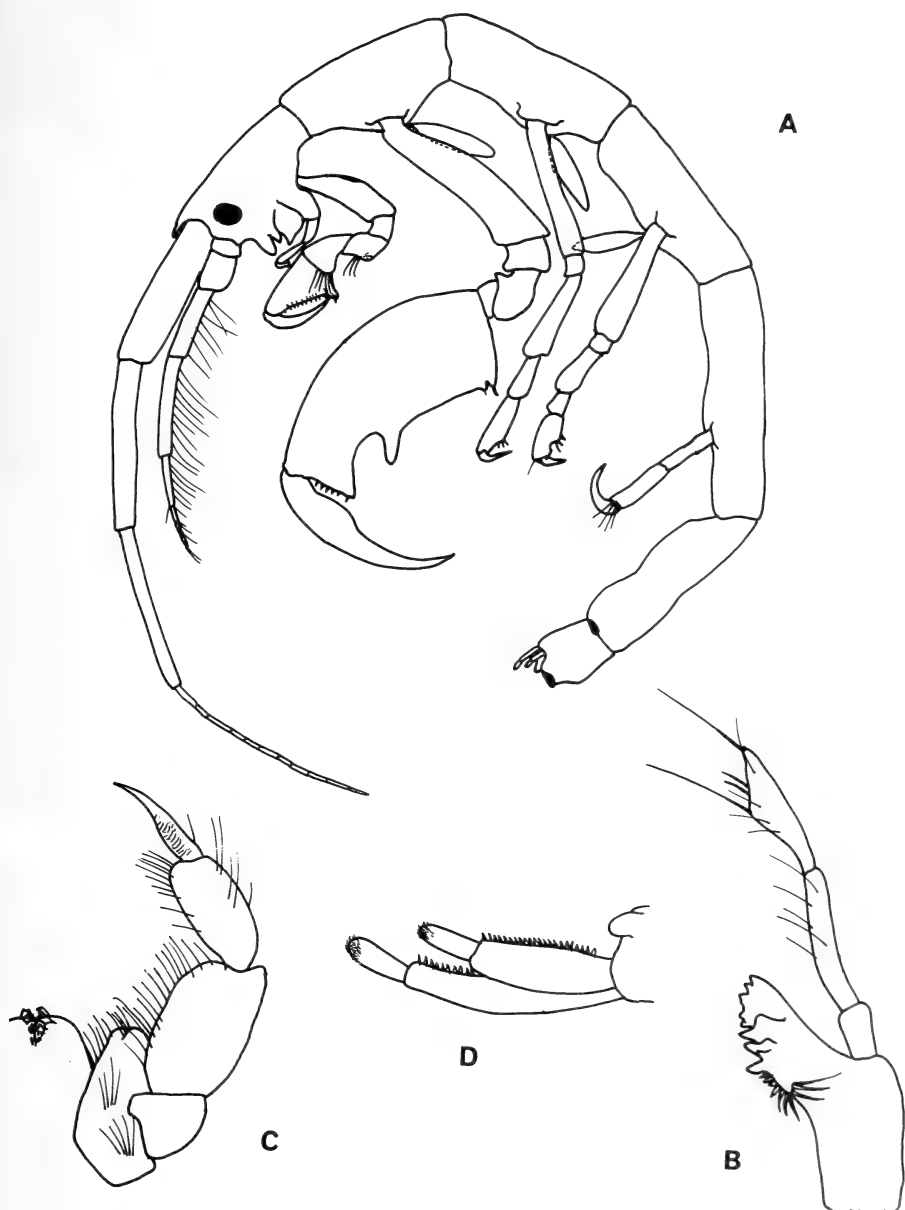


Fig. 7. *Chaka leoni* n. gen., n. sp.

Male, 11 mm: A—lateral aspect; B—mandible; C—maxilliped; D—lateral view of abdominal appendages.

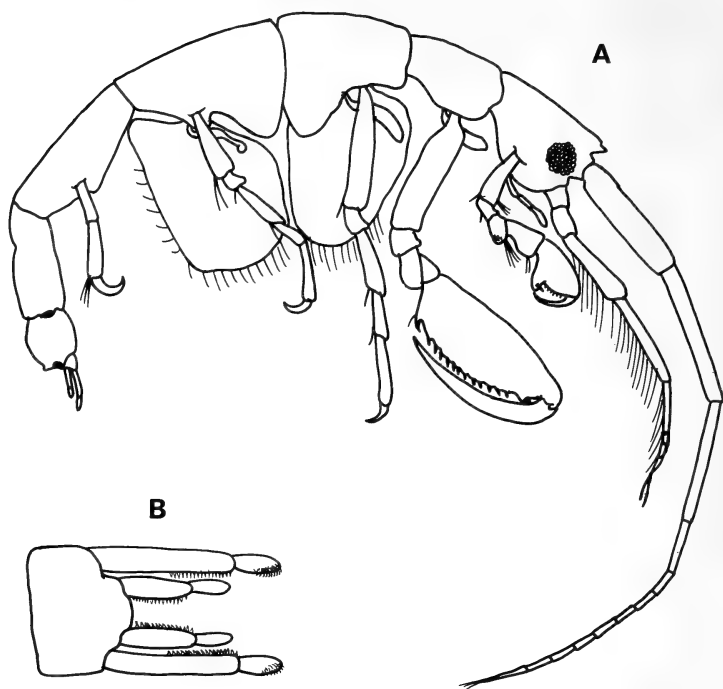


Fig. 8. *Chaka leoni* n. gen., n. sp.
Female, 8 mm: A—lateral aspect; B—dorsal view of abdomen.

1, flagellum 3-articulate, swimming setae present; mandible with 3-articulate palp, setal formula of terminal article 1-2-1, incisor of mandible (Fig. 7B) five toothed, lacinia mobilis smooth, two accessory plates present, below which lies a row of ten strong setae, molar absent; inner and outer lobes of maxilliped equal, inner lobes nearly fused, armed distally with serrate spines.

Propodos of gnathopod 1 subtriangular, palm evenly concave, defining angle produced into a rounded lobe; gnathopod 2 very large, propodos with proximal poison tooth followed by a pair of small protuberances, palm distally with a strong pointed tooth separated from a triangular tooth near the hinge by a semicircular excavation; dactyl strong, equal to palm; branchiae elongate-elliptical, three pairs found on pereon segments 2-4; pereopods 1 and 2 6-segmented, palm of propodos proximally with three spines; pereopod 3 3-segmented, propodos lacking palm and without spines; (pereopods 4 and 5 missing).

Abdomen with two pairs of bi-articulate appendages (Fig. 7D); article 1 of each dorsally with closely packed short spines set in a row, article 2 of each appendage distally finely setose.

Female: Rostral projection shorter and of different shape to that of the male;

antenna 2 as long as peduncle of antenna 1; propodos of gnathopod 2 smaller than that of male, palm evenly convex with a row of 12 short strong spines evenly spaced along its length and a small poison tooth at defining angle; pereopods as in male but 1 and 2 lacking spines; pereon segments 3 and 4 ventro-laterally produced into projecting keels, ventrally with large brood pouches; abdomen as in male.

Holotype: SAM A13165, male, 11 mm.

Type-locality: NAD 15K, 13 August 1958, 30°47'S/30°27'E, depth 36 m.

Material: Three males and three females from the type-locality.

SUMMARY

Data from the considerable collections amassed by the University of Cape Town Ecological Survey and the National Institute for Water Research have been incorporated with the records of previous authors in listing the known gammaridean and caprellid amphipod fauna of Natal. A total of 115 species is recognized from the area. Of these six species and one genus are described as new to science, namely *Microdeutopus thumbellinus* n. sp., *Unciolella spinosa* n. sp., *Ceradocus natalensis* n. sp., *Urothoe coxalis* n. sp., *Urothoe tumorosa*, n. sp., and *Chaka leoni* n. gen., n. sp., (Phtisicidae). In addition two existing species, *Gammaropsis imminens* K. H. Barnard and *Gammaropsis semidentatus* K. H. Barnard are synonymized with *Gammaropsis atlantica* Stebbing and *Gammaropsis holmesi* Stebbing respectively.

References to and distributions for each species are given, as well as brief diagnoses of those species not previously described in Parts 1 and 2 of this series.

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THE AMPHIPODA OF SOUTHERN AFRICA
PART 3
THE GAMMARIDEA AND CAPRELLIDEA
OF NATAL

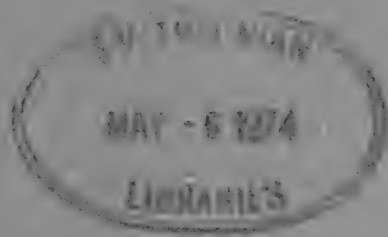
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By
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Cape Town Kaapstad

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BRIAN KENSLEY

South African Museum, Cape Town

(With 5 figures)

[*Ms. accepted 12 February 1974*]

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INTRODUCTION

When two species of *Callianassa* submitted to the South African Museum for identification proved to be problematic, it was decided to re-examine all the available mud-shrimp material from the west coast. As a result of this investigation, where previously three species were recorded from the area, five are now known, two of which have proved to be undescribed. In the accompanying figures, all dimensions are in millimetres.

DESCRIPTION

Callianassa adamas sp. n.

Figs 1, 2

Description

♂. Front of carapace evenly convex, rostrum a low rounded protuberance. First two abdominal segments more slender than following segments. Abdominal segments three to five with transverse band of short setae on mid-lateral areas. Eyestalks touching only at bases, tapering distally, reaching slightly beyond midpoint of 2nd antennular peduncle segment.

Antennule, peduncle three-segmented, basal segment somewhat shorter than 2nd segment, latter half length of distal segment.

Antenna, peduncle five-segmented, two distal segments subequal, three basal segments together equal in length to fourth segment.

Mandible, palp three-segmented, terminal segment bearing numerous curved spines, grading proximally into slender elongate spine-like setae. Incisor portion bearing nine well-separated teeth, molar portion consisting of single blunt tooth.

First maxilla, exopod shorter than outer endopod lobe, distally flexed.

Second maxilla, scaphognathite broadly oval.

First maxilliped endopod oval in outline, with broad band of densely packed setae on outer face. Exopod distally rounded.

Second maxilliped, dactyl with seven or eight spines on inner distal margin, one-third length of propodus. Latter distally swollen, bearing numerous elongate setae. Carpus very short, carpus and propodus together equal in length to merus, latter curved, with broad setal fringe on inner margin. Exopod leaf-shaped, curved, reaching to end of carpus.

Third maxilliped operculiform, propodus and carpus expanded, latter one-third longer than former, both with strong rounded longitudinal ridge on outer face. Merus and ischium together forming very broad plate-like structure, spines lacking on inner face.

First pereopod, smaller cheliped, dactyl slightly longer than palm, extending beyond fixed finger, cutting edge entire. Cutting edge of fixed finger with few tiny denticulations proximally. Carpus slightly more than twice longer than wide, merus and ischium narrower than carpus, ischium slightly longer than merus.

First pereopod, larger cheliped, three distal segments together $2\frac{1}{2}$ times mid-dorsal length of carapace. Dactyl extending beyond tip of propodal fixed finger, slightly more than half length of palm, distally strongly curved, cutting edge with strong rounded tooth proximally, another at about midpoint, inner surface with several scattered granules. Margin of fixed finger entire, with row of very faint granules on inner surface. Propodus ventrally carinate. Carpus a little longer than propodus and dactyl together, disto-ventral corner acute,

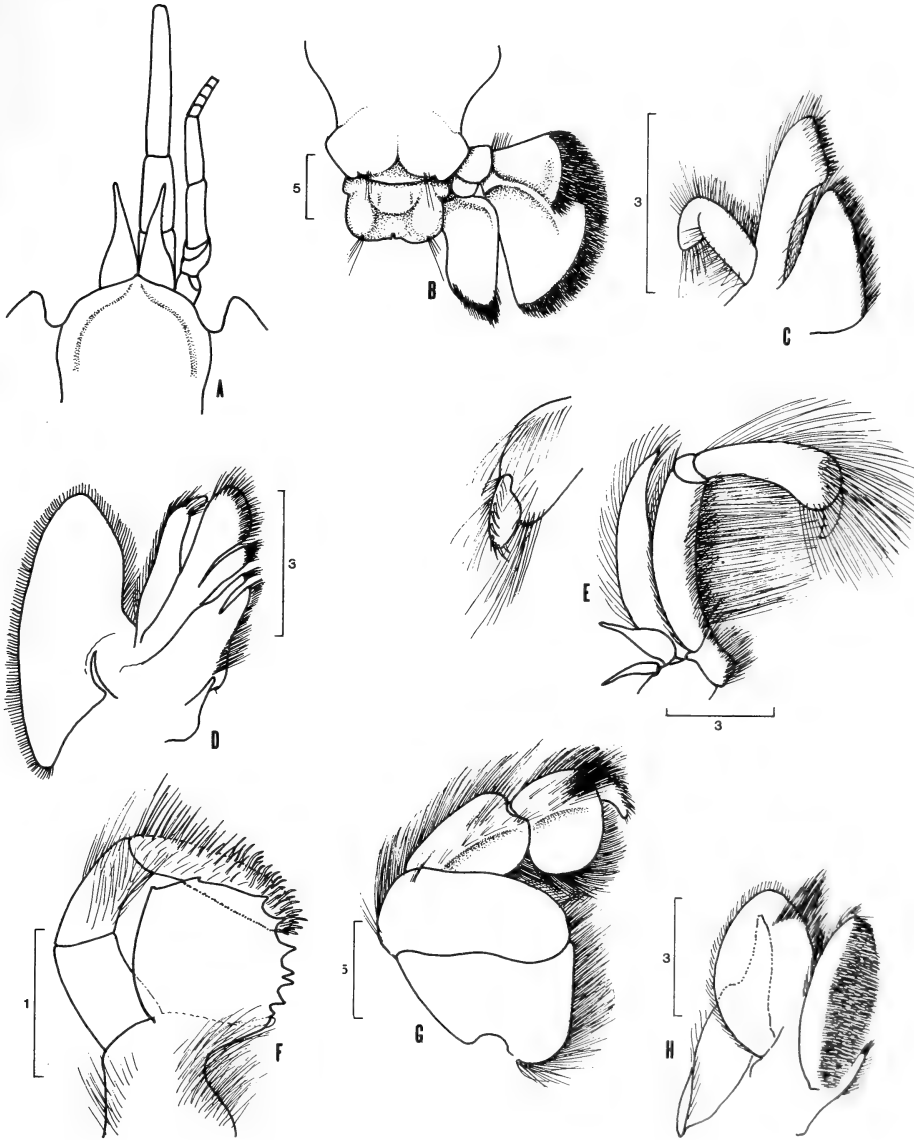


Fig. 1. *Callianassa adamas* sp. n. ♂. Holotype

A. Anterior carapace, antennae, and eyes in dorsal view. B. Telson and right uropod. C. First maxilla. D. Second maxilla. E. Second maxilliped with dactyl further enlarged. F. Mandible. G. Third maxilliped. H. First maxilliped.

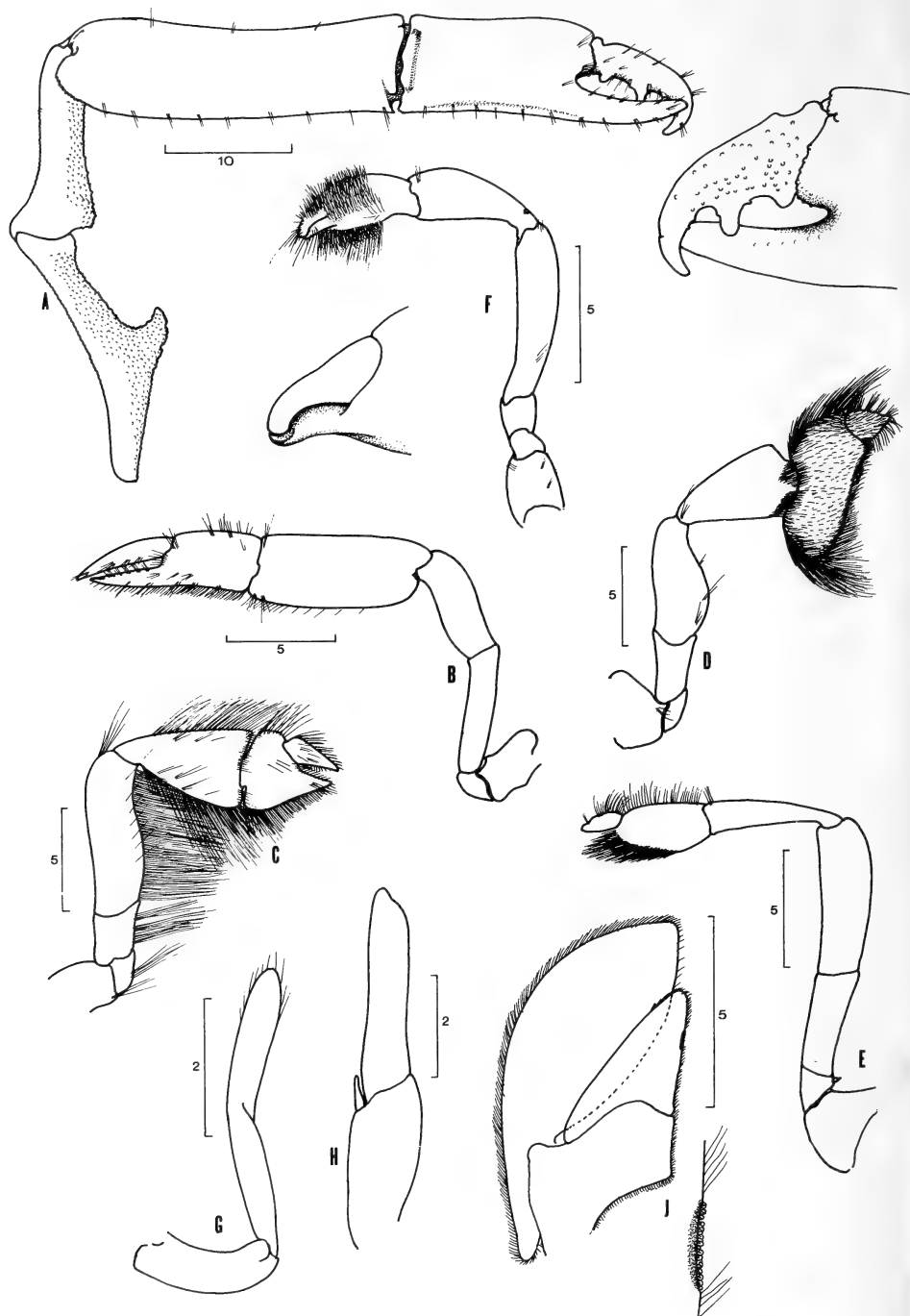


Fig. 2. *Callianassa adamas* sp. n. ♂. Holotype
 A. Large cheliped, with chela further enlarged. B. Smaller cheliped. C. Second pereopod.
 D. Third pereopod. E. Fourth pereopod. F. Fifth pereopod with chela further enlarged.
 G. First pleopod. H. Second pleopod. J. Third pleopod, with reduced appendix interna
 further enlarged.

disto-dorsal corner rounded, proximo-ventral corner evenly rounded, finely denticulate. Merus three-fifths length of carpus, ventral margin and part of outer surface granulate, proximo-ventral corner somewhat expanded into rounded crest. Ischium five-fourths length of merus, with broad hook-like process at midventral margin, most of outer surface granulate.

Second pereopod chelate, dactyl two-thirds length of propodus, latter broadly triangular. Carpus distally broadened, about three-quarters length of merus. Ventral margins of merus, carpus and propodus heavily setose.

Third pereopod dactyl and propodus heavily setose. Propodus produced into rounded-conical posterior lobe. Dactyl triangular. Carpus and merus subequal in length.

Fourth pereopod non-chelate, dactyl about half length of propodus, latter with dense disto-ventral setal 'brush'. Propodus two-thirds carpus length, carpus slightly shorter than merus.

Fifth pereopod chelate, dactylus one third total length of propodus. Dactyl and propodus apically spooned, rounded apical areas marked by minute row of denticles. Dactyl and distal portion of propodus heavily setose. Propodus and carpus equal in length, merus somewhat longer.

First pleopod two-segmented, basal segment slightly less than half length of distal segment. Latter flexed at about midpoint, bearing very few setae.

Second pleopod biramous, basopodite slightly less than length of inner ramus. Latter broad, tapering distally, outer ramus small, about one-sixth length of inner.

Third pleopod, inner ramus triangular, appendix interna reduced to a pad of rounded hooks on median margin of segment.

Uropod rami reaching well beyond telsonic apex. Inner ramus $2\frac{1}{2}$ times longer than wide, apically tapering, rounded. Outer ramus distally evenly convex, with broad band of short dense setae, and with median curved ridge.

Telson wider than long, with tiny medio-distal notch, proximally with median convex area, and two lateral convex areas.

♀. First chelipeds similar to smaller cheliped of male.

First and second pleopods as in male.

Material

Holotype	S.A.M.A12103	♂	C.L. 15,8 mm	T.L. 65 mm
Orange River mouth				
Allotype	S.A.M.A12103	♀	C.L. 14,0 mm	T.L. 58 mm
Orange River mouth				
Paratype	S.A.M.A10985	♂	C.L. 14,0 mm	T.L. 59 mm
Olifants River mouth				
Paratype	LBT.77A	♀	C.L. 12,9 mm	T.L. 51 mm
Lambert's Bay				

Numerous immature specimens with an average total length of 14 mm were obtained off Lambert's Bay. The shape of the eyestalks and telson, and the

appendages generally, indicate that these are probably juveniles of the present species.

The holotype and allotype were collected by the diamond dredge *Emerson-K* off the Orange River mouth in 1962, and were mentioned in a report on the material from the diamond grading grids by Grindley & Kensley (1966:9). The depth of the sampling was between 10 and 35 m. The female paratype and the numerous juveniles were obtained off Lambert's Bay by the Zoology Department of the University of Cape Town, using a suction sampling device. The material came from a depth of about 60 cm in the fine mud/silt substrate, in a water depth of 10–15 m. The male paratype was collected at the mouth of the Olifants River in 1960, but no depth or substrate information was recorded.

Remarks

The most striking feature of the present species is the elongate nature of the large cheliped of the male, quite unlike any species previously recorded from South Africa. Of the numerous species of *Callianassa* described from other parts of the world, only two would seem to have a similar elongate first cheliped. These are *C. major* Say, recorded from the eastern United States of America, especially the southern states where it occurs intertidally, and *C. islagrande* Schmitt, known from Louisiana.

Callianassa major can easily be separated from the present species on the basis of the large cheliped of the male. The dactylus of *C. major* possesses a single blunt tooth proximally on the cutting edge, as opposed to two large rounded teeth in the present species. The merus of the American species has a distinct triangular process on the proximo-ventral margin, whereas, although the merus of the present species is somewhat expanded proximo-ventrally, there is no distinct process. The telson of *C. major* would seem to be more rounded than *C. adamas*, while the eyestalks are relatively shorter in Say's species, reaching to the end of the first antennular peduncle segment. In the present species the eyestalks extend to beyond the middle of the second antennular peduncle segment.

The resemblance of *C. adamas* to *C. islagrande* is much greater; indeed, using both keys to the genus *Callianassa* from Florida provided by Biffar (1971), the species is run down to *C. islagrande*. From Schmitt's description (1935:5), and the rather inadequate photograph, several differences emerge on comparison with the present species. These are given in the following table, and would seem to warrant specific separation, not altogether surprising, the two species being separated by the width of the Atlantic Ocean.

	<i>C. islagrande</i>	<i>C. adamas</i>
Eyestalks	Twice as long as broad, contiguous to level of cornea	Three times longer than broad, contiguous only at bases, cornea not distinct

	<i>C. islagrande</i>	<i>C. adamas</i>
Antenna	Fourth peduncle segment reaching end of second antennular peduncle segment	Fourth peduncle segment reaching mid-point or slightly beyond, second antennular peduncle segment
Large Cheliped ♂	Merus with low denticulate/granulate tooth at posterior third Carpus finely denticulate on upper margin for almost whole length, lower margin with widely separate granules or denticles on distal four-sevenths Dactylus with conspicuous blunt right-angled tooth on upper border of terminal hook No strong rounded tooth at mid-point of cutting margin	Merus widened proximally, no distinct tooth Carpus weakly granulate on upper margin for proximal third, lower margin smooth No tooth on upper border of terminal hook Strong rounded tooth present at mid-point of cutting margin
Third Maxilliped	Fixed finger of propodus arises from deep sinus in palm Inner face of ischium with crescentic row of tiny granulations	Sinus at base of fixed finger barely apparent No granulations on inner face of ischium
Uropod	Inner ramus four times longer than wide	Inner ramus $2\frac{1}{2}$ times longer than wide

The specific name '*adamas*' is from the Latin for a diamond, the species having been caught on the Diamond Coast of South Africa.

Callianassa subterranea australis subsp. n.

Figs 3-5

Description

♂. Front with shallow rostrum, sides slightly concave, no lateral projections present.

Eyestalks medially contiguous, reaching almost to midpoint of second antennular peduncle segment. Pigmented area situated centrally. Antennule with two basal peduncular segments together equal in length to distal segment, peduncle reaching to about midpoint of third antennal peduncle segment.

Antennae with first three segments short, third with two squat spines distally, fifth segment about three-quarters length of fourth, both slender.

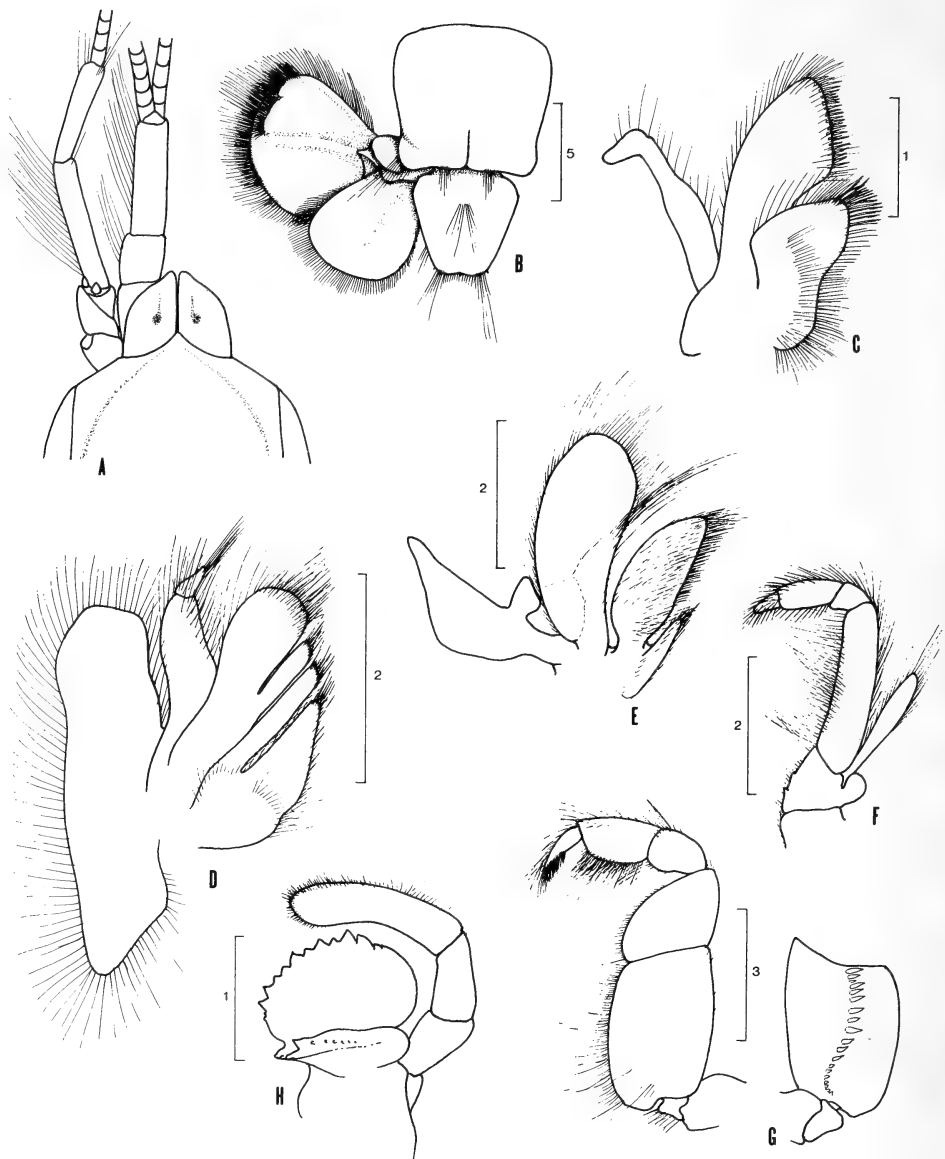


Fig. 3. *Callianassa subterranea australis* subsp. n. ♂. Holotype
 A. Anterior carapace, antennae, and eyes in dorsal view. B. Telson and left uropod. C. First maxilla. D. Second maxilla. E. First maxilliped. F. Second maxilliped. G. Third maxilliped, with inner view of ischium. H. Mandible.

Mandible with incisor portion bearing 12–13 strong teeth, molar portion with four strong teeth and row of six tiny denticulations. Palp three-segmented distal segment equal in length to two proximal segments together.

First maxilla, exopod slender, distally bearing flattened portion at right angles to rest of segment. Outer lobe of endopod, median margin bearing numerous short spines. Inner lobe bearing several serrate spines on median (inner) face. Second maxilla, exopod with short rough triangular distal segment, and elongate proximal segment.

First maxilliped, exopod distally rounded, fringed with setae. Epipod with small median lobe, and larger acute external lobe.

Second maxilliped, merus elongate, four times longer than wide, ischium bearing two small projections on inner margin, exopod three-quarters length of endopod merus.

Third maxilliped, merus and ischium broad, latter with sinuous row of about 15 or 16 strong conical denticles on inner surface.

First pereopod, smaller cheliped, dactyl and fixed finger of propodus slightly longer than palm, cutting margins entire. Carpus four times longer than wide, only slightly longer than propodus. Merus broad, margins convex. Ischium more slender than merus, slightly longer.

First pereopod, larger cheliped, dactyl strongly hooked, cutting edge bearing broad proximal very finely denticulate portion, followed by small blunt tooth. Propodus broad, fixed finger evenly curved, cutting edge entire, dorsal margin carinate, ventral margin finely crenulate. Dactyl and propodus together $2\frac{1}{2}$ times length of carpus, latter with proximo-ventral angle evenly and broadly rounded, finely crenulate, dorsally carinate. Merus slightly shorter than dorsal length of carpus. Dorsal margin with five small denticulations proximally. Ventral margin with strong denticulate hook-like process proximally, followed by denticulate convex crest.

Ischium and merus equal in length. Ischium proximally narrow, widening distally, ventral margin with about 10 small denticles, dorsal margin with hook-like process proximally.

Second pereopod chelate, propodus equal in length to carpus, merus somewhat longer; all three distal segments, and ventral margin of merus fringed with setae.

Third pereopod, dactyl slightly less than half length of propodus, covered with fine setae, elongate-triangular. Propodus with ventral margin bearing five isolated tufts of setae flanked by broad band of setae; posterior lobe not extending beyond ventral margin of carpus. Carpus about four-fifths length of merus, bearing distal setae.

Fourth pereopod non-chelate, dactyl about half length of propodus, covered with numerous setae. Propodus with ventral margin and external surface bearing three bands of dense setae.

Fifth pereopod with propodus, carpus, and merus elongate. Tiny chela formed by small dactyl and even smaller 'thumb' of propodus. Latter with dense pad of setae on distal outer surface.

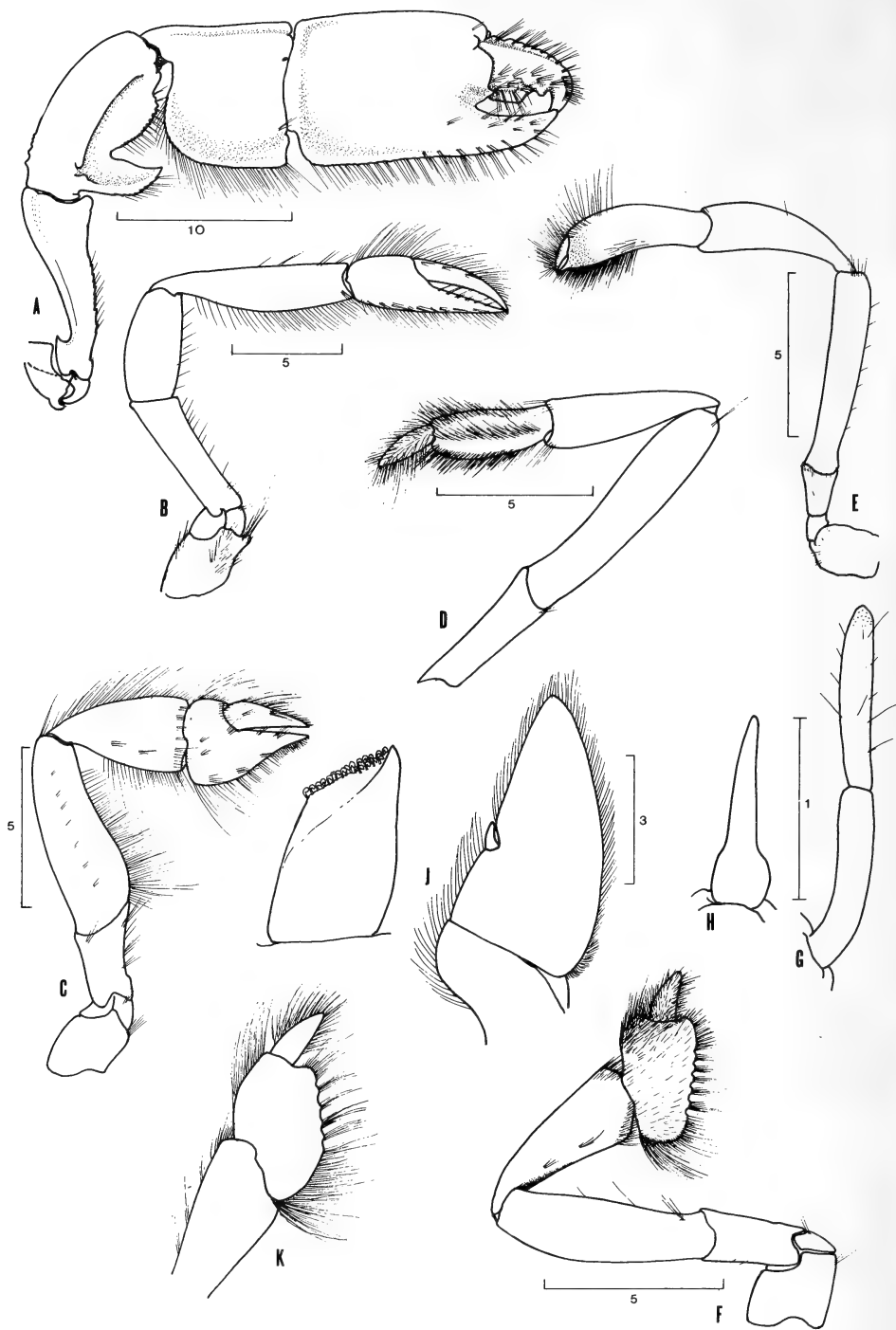


Fig. 4. *Callianassa subterranea australis* subsp. n. ♂. Holotype
 A. Larger cheliped. B. Smaller cheliped. C. Second pereiopod. D. Fourth pereiopod. E. Fifth pereiopod. F. Third pereiopod. G. First pleopod. H. Second pleopod. J. Third pleopod, with appendix interna further enlarged. K. *Callianassa subterranea subterranea*, two distal segments of third pereiopod.

First pleopod cylindrical, two-segmented, segments subequal.

Second pleopod consisting of single segment, basally swollen.

Third pleopod, endopod two-segmented, triangular, with appendix interna on median margin of distal segment, fringed with plumose setae.

Uropod with inner ramus distally rounded, only slightly longer than telson, longer than wide. Outer ramus with broad rounded ridge, distally rounded, bearing fringe of dense slender spines in addition to fringe of setae.

Telson distally truncate, with minute median and two lateral spinules, as long as wide, sides straight, converging distally.

♀. First pereiopod, larger cheliped, dactyl about equal to palm in length, slightly longer than fixed finger of propodus, evenly serrate on cutting edge. Fixed finger with cutting edge entire, distally slightly upturned. Lower margin of propodus finely serrulate, upper margin entire, carinate. Carpus slightly shorter than palm of propodus, proximo-ventral corner broadly rounded, margin finely serrulate. Merus equal in length to dorsal length of carpus, with four or five small denticulations on proximo-dorsal edge, ventral margin with broad hook-like process, ventrally denticulate, and with convex denticulate crest. Ischium longer than merus, ventral margin finely serrulate, distally broader than proximally.

First pleopod uniramous, two-segmented basal segment about half length of distal segment, slightly curved. Distal segment becoming leaf-like for slightly less than distal half, with rounded setae-bearing bulge at base.

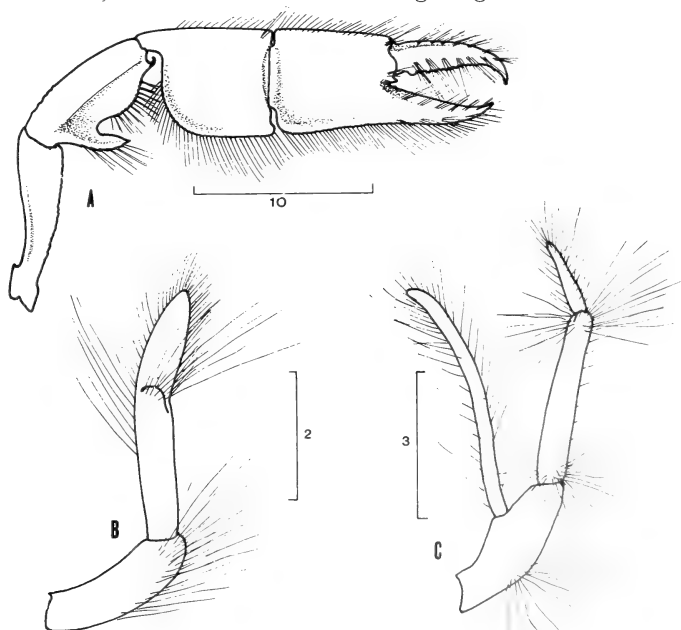


Fig. 5. *Callianassa subterranea australis* subsp. n. ♀. Allotype
A. Large cheliped. B. First pleopod. C. Second pleopod.

Second pleopod biramous. Basopodite broader than rami. Inner ramus of one segment elongate and slender. Outer ramus of two segments, basal segment twice length of distal, with rounded bulge distally, bearing elongate setae.

Material

Holotype	S.A.M.A13531	♂	C.L. 14,9mm T.L.	Lüderitzbucht
Allotype	S.A.M.A13532	♀	C.L. 13,8mm T.L. 50mm	Lüderitzbucht
Paratype	S.A.M.A13533	♂	C.L. 9,9mm T.L. 32mm	Lüderitzbucht
Paratype	S.A.M.A13534	♀	C.L. 12,3mm T.L. 41mm	Lüderitzbucht
Paratype	S.A.M.A12103	♀	C.L. 13,0mm T.L. 53mm	Orange River mouth

In addition, the following paratypes from Lüderitzbucht, in the collection of the Zoology Department, University of Cape Town, catalogue number SWD.5U: 7 ♂♂ T.L. range 34–48mm, 8 ♀♀ T.L. range 43–48mm

The Lüderitzbucht material was dredged from a depth of 180m by the *John D. Gilchrist* of the University of Cape Town, from a bottom of fine gravel and rock. The total length of the holotype cannot be given as the abdomen is detached.

Remarks

Of the four species of *Callianassa* recorded from South Africa only *C. rotundicaudata* does not possess a well-developed lobe on the propodus of the third pereiopod, as is the case in the present species. The shape and relative size of the telson, and the character of the larger cheliped of the male easily serve to separate these species.

The resemblance between the present species and *C. subterranea* (Montagu) known from the coasts of Great Britain, the Mediterranean, the North Sea, and the Atlantic coasts of Western Europe and North Africa (Poulsen 1940; De Man 1928) is unmistakable. From the full description of this species given by De Man (1928) and from comparison with material from Plymouth, England, only two differences emerge in the South African material. These are in the shape of the propodus of the third pereiopod, and in the larger chela of the male.

The propodus of the third pereiopod in *C. subterranea* has a posterior lobe somewhat rounded and tapered, while in the present material, the posterior lobe is relatively broader and squarer.

The larger chela in the male of the European species has the cutting edges of both the dactyl and the fixed finger unarmed except for some fine denticulations. This resembles very closely the larger cheliped of the female of the present material. In the male, however, the cutting edge of the dactyl in the larger chela possesses a strong flat-topped proximal tooth and a smaller rounded distal tooth.

With only these two differences, and with the almost identical structure of the body and all the other appendages, the close affinity between the European

and the South African species cannot be denied. With no records of *C. subterranea* between that in North Africa and the present South African records, it may be postulated that this is a case of antitropical distribution, with the southern form beginning to diverge from its (presumably) northern stock. With no further information available, it is perhaps best to designate the South African material as a different subspecies from the European form. Thus the latter is *Callianassa subterranea subterranea*, while the form here described is *Callianassa subterranea australis*.

KEY TO THE SOUTH AFRICAN SPECIES OF *CALLIANASSA*

1. Third pereopod with propodus produced into well-developed T-shaped or hammer-headed posterior lobe 2
- Third pereopod with posterior portion of propodus not produced 4
2. Inner ramus of uropod oval, extending well beyond telsonic apex 3
- Inner ramus of uropod distally square, not extending beyond telsonic apex *natalensis*
3. Third, fourth, and sixth segments of third maxilliped expanded
- Large chela with strong blunt proximal tooth on dactyl *kraussi*
- Third, fourth, and sixth segments of third maxilliped not expanded
- No strong blunt proximal tooth on dactyl of large chela *gilchristi*
4. Uropods extending well beyond telsonic apex
- Dactyl of large chela in male lacking broad flat-topped proximal tooth 5
- Uropods not extending well beyond telsonic apex
- Dactyl of large chela in male with broad flat-topped proximal tooth *subterranea australis*
5. Telson distally evenly rounded
- Ischium of larger cheliped in male lacking ventral hook-like spine *rotundicaudata*
- Telson distally broadly bilobed
- Ischium of larger cheliped in male with broad ventral hook-like process *adamus*

DISTRIBUTION OF THE SOUTH AFRICAN SPECIES OF *CALLIANASSA*

<i>C. adamas</i> sp. n.	Orange River mouth, Olifants River mouth, Lambert's Bay, 10–35m depth
<i>C. gilchristi</i> Barnard	Saldanha Bay, False Bay to Durban, 36 m depth
<i>C. kraussi</i> Stebbing	Saldanha Bay, False Bay to Zululand
<i>C. natalensis</i> Barnard	off Natal
<i>C. rotundicaudata</i> Stebbing	Orange River mouth, Saldanha Bay, False Bay, Algoa Bay, 10–35m depth
<i>C. subterranea australis</i> subsp. n.	Lüderitzbucht, Orange River mouth, 10–180m depth

SUMMARY

A new species and a new subspecies of the mud-shrimp genus *Callianassa* is described from the west coast of South Africa. The six southern African species of *Callianassa* are reviewed, and a key to the species is provided.

ACKNOWLEDGEMENTS

I am grateful to Dr R. W. Ingle of the British Museum (Natural History) for making specimens of *Callianassa subterranea* available for comparison, and for his critical reading of the manuscript, and to Professor J. H. Day and Mr N. Christie of the Department of Zoology of the University of Cape Town for providing material of both the new species and new subspecies here described.

GAZETTEER

Algoa Bay	33.58S., 25.36E.
Durban	29.53S., 31.00E.
False Bay	34.12S., 18.56E.
Lambert's Bay	32.04S., 18.20E.
Lüderitzbucht	26.38S., 15.10E.
Olifants River mouth	31.42S., 18.13E.
Orange River mouth	28.38S., 16.27E.
Saldanha Bay	33.00S., 17.56E.

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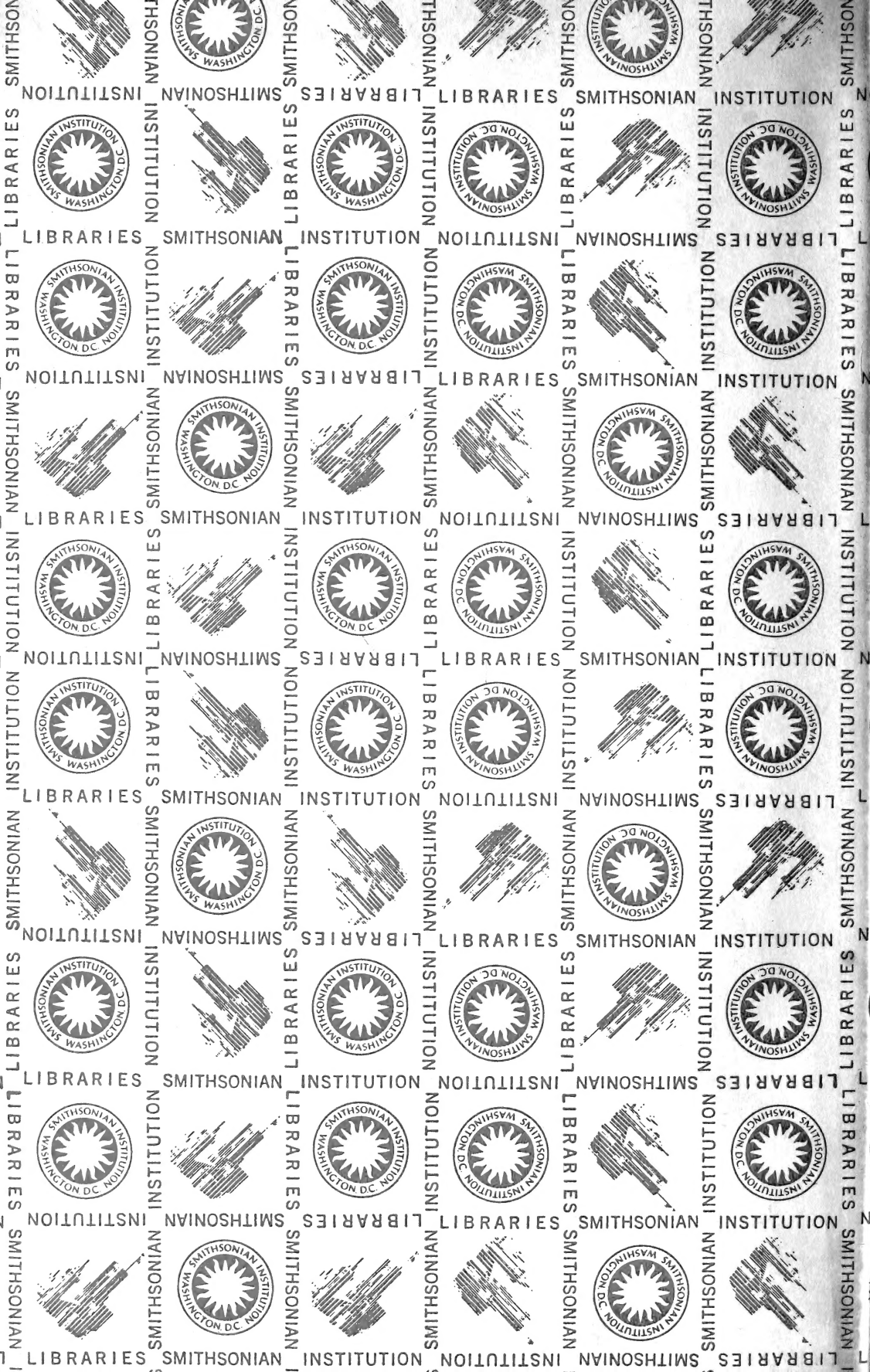
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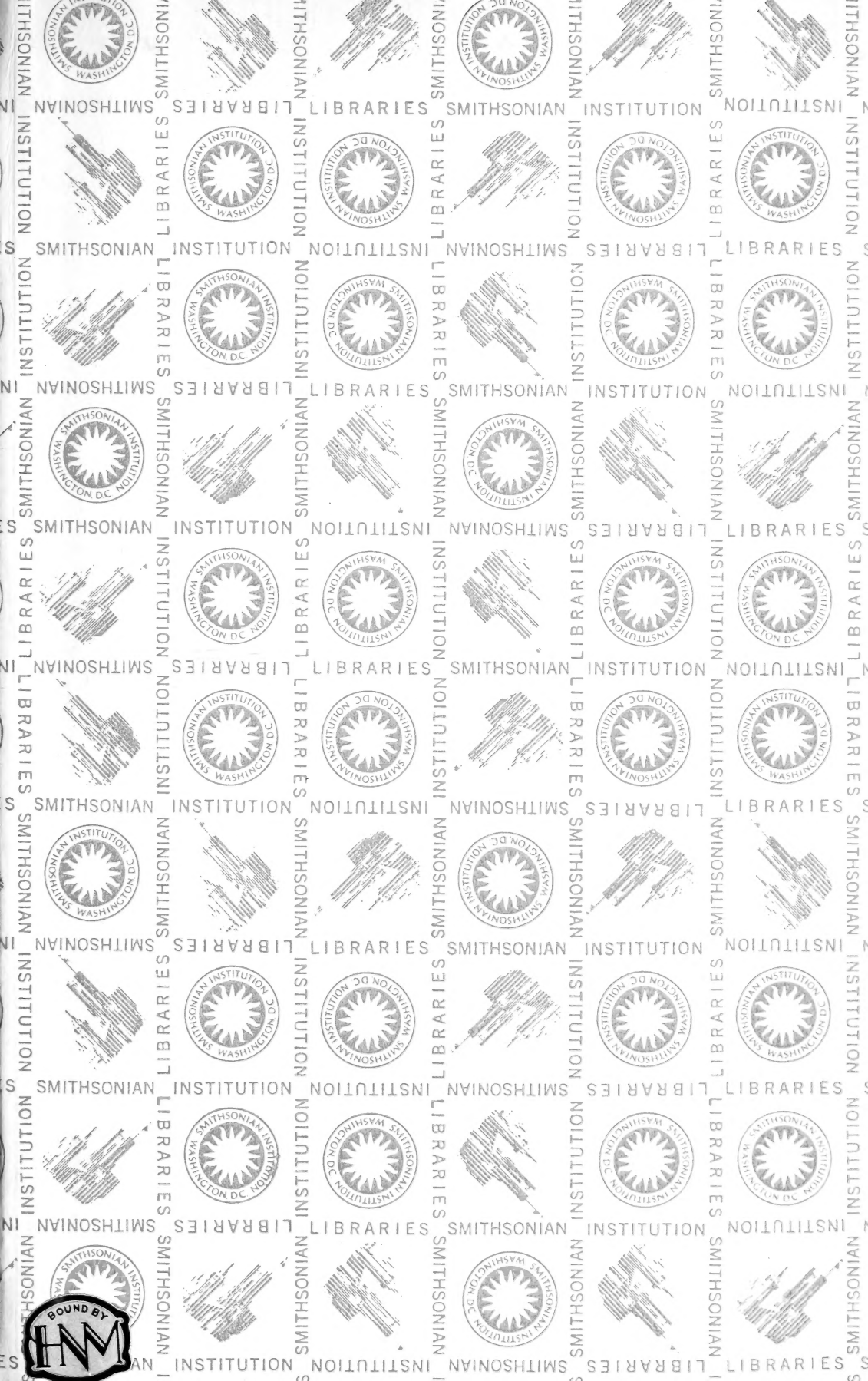
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Brian Kensley

THE GENUS *CALLIANASSA* (CRUSTACEA,
DECAPODA, THALASSINIDEA)
FROM THE WEST COAST OF SOUTH AFRICA
WITH A KEY TO THE SOUTH AFRICAN SPECIES







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